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The role of the Pacific sand dollar (Dendraster excentricus) in intertidal benthic community structure

University — Université

University of Alberta

Degree for which thesis was presented — Grade pour lequel cette thèse fut présentée

Ph.D.

Year this degree conferred — Année d'obtention de ce grade

1980.

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THE UNIVERSITY OF ALBERTA

THE ROLE OF THE PACIFIC SAND DOLLAR, DENDRASTER EXCENTRICUS, IN INTERTIDAL BENTHIC COMMUNITY STRUCTURE

by

ANNETTE L. SMITH

(C)

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

ZOOLOGY

EDMONTON, ALBERTA

1980

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled The Role of the Pacific Sand Dollar, Dendraster excentricus, in Intertidal Benthic Community Structure

submitted by Annette L. Smith

in partial fulfilment of the requirements for the degree of Doctor of Philosophy

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Supervisor

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External Examiner

Date May 18th, 1979

Dedication

To my husband, Peter,

who not only gave his support and encouragement throughout the course of this study, but expressed his devotion by spending three winters carrying wet sand across tidal flats at midnight.

Abstract

The role of Dendraster excentricus in the intertidal community was investigated using multivariate analyses of sampling data and field experiments.

The infauna inside and outside sand dollar beds on ten beaches were sampled, and several statistical techniques were used to detect a "sand dollar bed community". Cluster analysis did not suggest such a community. Contingency tables of co-occurrences revealed no species either positively or negatively associated with Dendraster. However, the bivalve Transennella tantilla, the tubicolous crustaceans Corophium spp., Ampelisca agassizi, and Leptochelia savignyi, and the polychaetes Glycinde polygnatha and Malacoceros arenicola were significantly more numerous inside than outside the sand dollar beds, while the polychaete Armandia brevis was more abundant inside the beds. Significantly fewer tube-building animals occurred inside sand dollar beds than outside.

The infauna at ten stations on one beach were sampled quarterly for two years. Cluster and discriminant analyses and analyses of variance suggested that the fauna of the sand dollar bed stations differed from that of the stations without Dendraster. Principal component analysis revealed an assemblage of tube builders in stations without Dendraster. Strong seasonal variations in the infaunal community were demonstrated by all statistical techniques.

The effect of Dendraster on infaunal species was tested by manipulating sand dollar densities. Covariance analyses showed that the abundances of T. tantilla, several species of tube builders, including L. savignyi and Malacoceros fulginosus, and an amphipod decreased significantly with increasing numbers of sand dollars, while another amphipod and a polychaete increased their numbers at intermediate densities of Dendraster. Removal of Dendraster from dense beds was followed by increases in numbers of tube builders.

It proved impossible to separate the effect of sediment disturbance by Dendraster from the effect of the sand dollars' occupying space. Neither the addition of the tests of dead sand dollars nor hand disturbance of the sediment brought about decreases in tube builder populations equal to those caused by live Dendraster.

It is concluded that sand dollars contribute to intertidal community structure by limiting the distribution of tube builder assemblages. Dendraster appears to be a dominant spatial competitor, which not only occupies space near the sediment surface, but whose burrowing activity interferes with other organisms.

Acknowledgments

I wish to thank my supervisory committee, Drs. F. S. Chia, J. C. Holmes and J. Addicott for their encouragement and suggestions. Dr. Holmes and Dr. S. A. Woodin were particularly helpful in providing constructive criticism of an earlier draft of this manuscript.

The facilities of the Friday Harbor Laboratories were kindly made available to me by the director, Dr. A. O. D. Willows. Thanks are also due to Drs. R. F. Scagel and R. E. Foreman of the University of British Columbia and Drs. M. Mackauer and P. V. Fankboner and Ms. C. Thompson of Simon Fraser University, who provided me with laboratory space and access to computing facilities.

I wish to express appreciation to Mr. and Mrs. L. A. Stone and Mr. R. C. McKay, who allowed access to private tidelands on East Sound.

The computer programs for clustering by information gain and for the contingency tables of species co-occurrences were made available to me by Dr. R. E. Foreman. The BMDP statistical package (Dixon and Brown 1977) was developed at the Health Sciences Computing Facility of the University of California at Los Angeles sponsored by NIH Special Research Grant RR3. Dr. J. D. Popham provided helpful suggestions for the multivariate analyses of the data.

I am grateful for the assistance with taxonomy given by Craig Staude, who identified most of the amphipods, and Dr.

K. Fauchald, who helped with identification of the polychaetes. Any mistakes are my own.

Drew Harvell helped to collect field data and to sort samples, and Bob Burke surveyed the elevations of the sampling stations in False Bay. Their assistance is sincerely appreciated.

The final draft of this thesis could not have been formatted on the computer without the help of Ms. Coleen Melsness.

This research was supported, in part, by a National Research Council Scholarship and a University of Alberta Dissertation Fellowship to the author and a National Research Council grant to Dr. F. S. Chia.

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I. General Introduction

Recent investigations in marine ecology have emphasized the roles of biological agents in organizing benthic communities. Field experiments have confirmed that interspecific competition and predation are important structuring forces on rocky intertidal shores (Connell 1961a, 1961b, 1970; Dayton 1971; Paine 1971, 1974).

Traditional studies of soft sediment communities have stressed the description of faunal associations and their distributions. The earliest investigators defined communities by naming their two dominant species (Shelford et al. 1935; reviews by Jones 1950, Thorson 1957). Subsequent workers have employed measures of diversity (Sanders 1968) and multivariate statistical techniques (Cassie and Michael 1968, Lie and Kelley 1970, Lie and Kisker 1970, Stephenson et al. 1970, 1972; Popham and Ellis 1971) to separate communities based on all but the rare species in the associations. Many studies have noted that the distributions of species and communities are limited by sediment grain size, with associations found in sand differing from those in mud (Sanders 1958, Cassie and Michael 1968, Nichols 1970, Eleftheriou and Nicholson 1975).

However, some investigators have commented on the importance of biological factors in structuring soft-sediment communities. As early as 1935 MacGinitie noted that no animals inhabiting fixed tubes or burrows occurred in beds of Callianassa, where the soil was unstable, but

that worms without permanent burrows were more abundant there than elsewhere. Rhoads and Young (1970) extended this type of observation to propose their theory of "trophic group amensalism": that deposit feeders produce unstable sediments which are unsuitable for the survival of suspension feeders. Others have observed that tube builders stabilize sediments and increase environmental complexity, providing habitats for other species (Fager 1964, Mills 1967, Rhoads and Young 1971, Young and Rhoads 1971).

In the last few years, investigators have employed experimental techniques to study biological interactions among soft-sediment organisms. In the laboratory Levinton (1977) observed direct interference between protobranch bivalves, with Yoldia limulata disrupting the burrows of Solemya velum. Using caging and other manipulative field experiments, Woodin (1974) and Petersen (1977) have demonstrated the importance of interspecific competition, and Young et al. (1976), Virnstein (1977), Wiltse (1977) and Bell and Coull (1978) have elucidated the role of predation in intertidal and subtidal soft-bottom communities. Virnstein (1977), Wiltse (1977), Orth (1977) and Woodin (1978) have also discussed the contribution of bioturbation to soft-sediment community structure.

Thus, it appears worthwhile to look further for organisms which play major structuring roles in the benthic community. Any large organism which occurs in high densities might be a dominant force in benthic associations.

The Pacific sand dollar, Dendraster excentricus (Eschscholtz), is such an organism. Sand dollars occur in dense aggregations, sometimes reaching more than 1000 animals/m^2 (Merrill and Hobson 1970, Timko 1975). On the outer coast their distribution is primarily subtidal (McCauley and Carey 1967, Merrill and Hobson 1970), but in protected waters they occur intertidally (MacGinitie and MacGinitie 1968), where they may reach densities exceeding 600 animals/m^2 (Birkeland and Chia 1971).

Such dense aggregations of sand dollars could influence other benthic organisms in one or more of three different ways. Sand dollars might create a community by providing a substrate or hiding places for epifauna (Merrill and Hobson 1970, J. Morin, personal communication). Alternatively, by occupying most or all of the surface area of the sand dollar bed, they might eliminate infaunal species which require access to the sediment surface.

Dendraster could also affect community structure by reworking the sediments. Rhoads (1967) includes displacement of particles by an organism moving over or through the sediment in his definition of reworking. Sand dollars moving on the sediment surface leave a characteristic trail in the sand (Chia 1969; Figure 1). Intertidal sand dollars sit inclined above the sediment surface to feed at high tide and bury themselves as the tide recedes (MacGinitie and MacGinitie 1968), burrowing to depths as great as 10cm (Chia 1969). The resulting frequent sediment turnover could

Figure 1. Characteristic trail left by a sand dollar moving near the sediment surface. Photograph courtesy of F. S. Chia.

displace smaller intertidal organisms dwelling in the upper layers of sediment. Thus, bioturbation by Dendraster could limit the distributions of some species.

In the following study I attempt by traditional sampling and statistical analyses to demonstrate whether a definible intertidal sand dollar bed community exists, and by manipulative field experiments to determine the role of Dendraster excentricus in the benthic community.

II. The Communities of Ten Sandy Beaches in Puget Sound and the Strait of Georgia, with Reference to Sand Dollar Beds

A. Introduction

Experimental studies of species interactions are often useful to understand community structure, but definition of the community must precede experimentation. Benthic communities are traditionally defined by surveys of the fauna and recognition of species which regularly co-occur. Petersen (1918) first described marine benthic communities by naming two dominant species. More recent investigators have employed statistical techniques including recurrent group analysis (Fager 1957), principal components analysis (Cassie and Michael 1968), cluster analysis (Stephenson et al. 1970) and factor analysis (Lie and Kelley 1970) to separate faunal associations.

Only a few studies of the soft sediment benthic assemblages of the northern Pacific coast of North America have been published, and most of these describe subtidal habitats. In a series of papers, Lie and some colleagues (Lie and Kelley 1970, Lie and Kisker 1970, Lie 1974) employed factor analysis to define three communities associated with different depths and sediment types in Puget Sound and off the coast of Washington. Nichols (1970) conducted a similar study of small scale changes in polychaete assemblages in Port Madison, Washington. Ellis (1971) reviewed his own and others' surveys of the infaunal

communities of the Strait of Georgia, relating these associations to the parallel community concept of Thorson (1957). Popham and Ellis (1971) used cluster and ordination analyses to separate pelecypod assemblages on a sandy shelf in the Strait of Georgia.

Most studies of the intertidal fauna of this region have been qualitative. Shelford et al. (1935) surveyed the intertidal, as well as subtidal sediments of the San Juan Islands, naming the communities in the Petersen tradition as Macoma-Paphia (=Protothaca) and Macoma-Leptosynapta associations. Wieser (1959) collected the smaller infauna from five beaches in Puget Sound and related the distributions of individual species to sediment grain size. Armstrong et al. (1976) also surveyed five Puget Sound beaches, providing faunal lists and relative abundances (but no numbers) of each species. While conducting primarily a geological survey of Boundary Bay, Kellerhals and Murray (1969) differentiated between a sand dollar community and an eelgrass community, naming some of the macrofauna associated with each. Levings and Coustalin (1975), however, provided counts and biomasses of the species they encountered on transects of the Sturgeon and Roberts Banks regions of the Fraser River Estuary.

Sand dollars (Dendraster excentricus) occur at high densities in Puget Sound (Birkeland and Chia 1971) and may play a dominant role in the organization of intertidal communities of this region. They are large animals which

alter sediment stability by their burrowing activity. Several authors (Rhoads and Young 1971, Woodin 1978) have shown that species displaying such characteristics have important effects on soft-sediment community structure.

Before proceeding with an experimental study of the role of Dendraster, it is necessary to document that the fauna of sand dollar beds differs from the fauna of adjacent areas of sand outside the beds. Merrill and Hobson (1970) have listed species which are more numerous in subtidal sand dollar beds than in adjacent sediments, but apart from that study and the observation of Kellerhals and Murray (1969) no such documentation has been published. I have, therefore, sampled the infauna of the sand dollar beds and adjacent sediments on the beaches in Puget Sound and the Strait of Georgia and used several statistical techniques in an attempt to define a "sand dollar bed community", or at least to recognize species positively and negatively associated with Dendraster.

This study should also provide some quantitative information on the intertidal sand flat fauna of this region, but since each site was sampled only once, the descriptions of the fauna of these beaches must be considered preliminary.

B. Methods and Materials

Study Sites

The infauna were collected inside and outside the sand dollar beds on ten beaches from southern Puget Sound to Hornby Island in the Strait of Georgia (Figure 2) . Each site was sampled once at low tide in late July or August, 1977.

The sand dollar bed at Tolmie State Park lies largely in the public recreation area. On one side it is bordered by a small stream flowing into the sound; on the other it extends onto private beaches. On the day of the sampling, the bed and adjacent sand flat were covered with a thick mat of drift algae. Many recently-dead sand dollars were present.

At Puget City the sand dollar bed is limited on one side by rock and terminates on the other side at the boat launching ramp of a marina. The bed is patchy, with dense aggregations of Dendraster and areas of unoccupied sand. On the day of sampling, an oily smell was noticible in the area.

The Dendraster bed at Alki South has been described by Birkeland and Chia (1971). The sand dollars are aggregated in pockets of sand between cobble. The bed terminates on one side where the sediment becomes hard-packed clay, while the opposite edge apparently occurs at a mat of tubes.

The sand dollar bed at Alki North is confined to a water-filled channel behind a large sand bar. The bed is

Figure 2. Map of Puget Sound and the Strait of Georgia, showing sampling sites. Names of the locations are abbreviated as follows:

TP = Tolmie State Park
PC = Puget City
AS = Alki South
AN = Alki North
BB = Buck Bay
FB = False Bay
WR = White Rock
CB = Crescent Beach
QB = Qualicum Beach
HI = Hornby Island

HI
QB
STRAIT of GEORGIA
CB
WR
VANCOUVER ISLAND
BB
FB
STRAIT of JUAN DE FUCA
PUGET SOUND
AN
AS
PC
TP

discontinuous, more resembling a series of separate beds, with clusters of Dendraster separated by long stretches of unoccupied sand. Within the clusters, sand dollar densities are visibly higher than those reported by Birkeland and Chia (1971).

At Buck Bay the sand dollars occupy the center of a small sand flat. The bed has sharp lateral and seaward margins which do not correspond with any obvious physical features.

The Dendraster bed at False Bay is sparse and discontinuous, occupying the channels behind four sand bars at the southern margin of the bay. This site has been described in detail by Pamatmat (1966).

The Crescent Beach sand dollars are similarly distributed discontinuously in channels behind a series of sand bars. Eel grass (Zostera) is present near many of the patches of Dendraster, as are accumulations of empty tests and bivalve shells.

I found only a few sand dollars at White Rock, on the sand flat near Semiahmoo Park. All the Dendraster were discovered in a few square meters in a channel between the series of sand bars which are characteristic of this beach. All were six to seven centimeters in diameter and possibly represented a single successful recruitment in this area.

The sand dollar bed at Qualicum Beach extends along most of the public beach but is patchy, with areas of unoccupied sand separating aggregations of Dendraster. The

sediment surface is rippled, and when buried the sand dollars are invisible under the ripple.

On Hornby Island the Dendraster bed extends the full length of Tribune Bay, broken only by a few patches of unoccupied sand. The sediment is rippled, and the sand dollars are buried deeply and invisible under the ripple.

All of the beaches except False Bay and Buck Bay are subject to heavy recreational use. The tide flat at Buck Bay is privately owned, and the owners and their friends occasionally dig clams there. False Bay is owned by the University of Washington, and the tidal flat is used for research and teaching.

Sampling Method

The infauna were collected in 10 X 10 X 10cm cores of sand. Three cores were taken inside and three outside each sand dollar bed. Inside each bed the cores were taken within a 3-m radius at an apparently dense part of the bed near an edge. Within the designated area, random positions of the cores were determined by the rapidly rotating investigator technique of Sanders et al. (1961), except that in patchy beds cores were not taken in areas unoccupied by Dendraster. In particularly sparse beds (Crescent Beach, White Rock) cores were taken near obvious aggregations of sand dollars.

The positioning of cores outside each sand dollar bed was determined by the configuration of the bed. Where the bed had a clear edge (Tolmie State Park, Alki North, Alki

South, Buck Bay), the cores were taken within a 3-m radius just beyond the edge and at the same tide level as the bed, but areas clearly uninhabitable by Dendraster (eg., the fresh water inflow at Tolmie State Park) were avoided. Where the bed was sparsely populated and patchy (False Bay, Crescent Beach, White Rock), the samples were taken approximately 50m down the beach at the same tide level as the bed, in areas without sand dollars. At the remaining sites, where Dendraster extended through all of the habitable area, the samples were collected from unoccupied patches of sand surrounded by the beds.

A single additional sample was collected inside and outside each bed for sediment analysis. This collection was made by scooping out sand to a depth of 10cm with a garden trowel. The samples were placed on ice and frozen upon return to the laboratory.

The sand dollar density in each bed was measured by counting all adults found to a depth of 10cm in five $0.25m^2$ patches. These patches were selected by placing a wooden frame near the three sites from which the infauna had been collected. Two random positionings of the frame within the 3-m collection radius were also counted.

The infaunal samples were fixed in 10% formalin for at least 24 hours. They were then washed through a 500μm sieve. Material retained on the screen was transferred to 70% alcohol.

The animals were sorted and enumerated using a

dissecting microscope. Only whole animals and fragments with heads were counted. Nematodes, copepods, and ostracods were considered large representatives of the meiofauna and were ignored.

The sediments were dried at 100C for 24 hours and divided into portions for grain size and organic carbon analyses. Grain size was determined by mechanically shaking the sediment for 10 minutes through a Wentworth series of sieves. The mean grain size and sorting coefficient were determined graphically as suggested by Hulings and Gray (1971). The silt-clay content was also recorded. The organic carbon content was calculated as ash-free dry weight after ignition of the sediment at 500C for one hour. While not as accurate as a carbon analyzer, this method is generally adequate for determination of organic carbon in marine sediments (Byers et al. 1978).

Statistical Analysis

A number of statistical techniques were employed in the attempt to detect a sand dollar bed community and to determine the effect of *Dendraster* on community structure.

Cluster analysis was used to detect any pattern in the distributions of species which might represent communities. All species which were found at three or more sites, plus species of which ten or more individuals occurred at one site, were included in the analysis. Counts of the three faunal samples inside each sand dollar bed were pooled, as

were the three outside samples, and the resulting 20 stations were clustered using information content as the index of similarity. This measure, described by Stephenson et al. (1970), based on the method of Williams et al. (1966), calculates the similarity between two sites as information gain based on the Shannon information content. The stations were also clustered according to their sediment characteristics (listed in Table 1), using the Euclidean distance measure, which is appropriate for continuous data. The computer program for the latter clustering method was BMDP:2M (revised December, 1977) from the BMDP statistical package (Dixon and Brown 1977).

In order to detect individual species which might be positively or negatively associated with sand dollars, chi-square values were calculated from 2 x 2 contingency tables, using the presence/absence of each species and Dendraster. The three samples from each station were pooled for this analysis.

The Shannon-Weaver diversity values and equitability (the ratio of the measured diversity to the maximum diversity possible in a collection containing N individuals) were calculated for each station using the pooled samples. The computer program for these functions was obtained from Orr et al. (1973). The differences in diversity, equitability and the number of species present inside and outside sand dollar beds were compared using paired t-tests.

The numbers of some abundant species and of pooled

Table 1. Characteristics of sediments inside (+) and outside (-) ten sand dollar beds. Mean grain size and sorting coefficient are given in phi units.

Location	% Organics +	% Organics -	Mean Grain Size +	Mean Grain Size -	Sorting Coefficient +	Sorting Coefficient -	%Silt Clay +	%Silt Clay -
Tolmie State Park	0.49	0.57	2.04	2.13	0.63	0.66	2.2	2.1
Puget City	0.56	0.47	1.48	1.48	0.77	0.83	1.1	1.3
Alki South	0.48	0.29	1.81	1.65	0.72	0.84	2.4	1.2
Alki North	0.51	0.53	2.14	2.19	0.69	0.70	2.1	2.0
Buck Bay	0.50	0.55	2.23	2.52	0.74	0.52	1.6	0.8
False Bay	0.60	0.37	2.48	2.28	0.39	0.62	0.4	0.6
White Rock	0.26	0.27	2.56	2.64	0.37	0.35	0.2	0.2
Crescent Beach	0.50	0.30	1.97	1.83	0.57	0.56	1.1	0.8
Qualicum Beach	0.24	0.22	2.48	2.63	0.64	0.58	0.4	1.9
Hornby Island	0.23	0.26	2.51	2.57	0.31	0.32	0.1	0.2

tube-building animals and motile crustaceans (amphipods, except tubicolous species, cumaceans and crabs) inside and outside the sand dollar beds were compared with two-way factorial analyses of variance of the replicated data. The counts in each of the three cores were transformed using ln(x+1) prior to these analyses in order to normalize the distributions.

C. Results

All of the beaches sampled have a similar fauna, with four species which comprise at least 5% of all individuals observed (excluding False Bay, where faunal densities are an order of magnitude higher than those of any other site) occurring at seven of the ten locations (Table 2). These species are the bivalve Mysella tumida, the cumacean Cumella vulgaris, the amphipod Synchelidium shoemakeri, and the polychaete Scoloplos armiger. Two other polychaetes, Nephthys caeca and Glycinde polygnatha, each total more than 1% of all individuals observed and are present on seven beaches. Tubicolous amphipods of the genus Corophium make up more than 5% of all individuals and were collected on six beaches.

The cluster analysis of the species data (Figure 3) does not suggest a "sand dollar bed community". The two stations at False Bay differ from all other sites. The remaining sites are divided into two major groups, the

Table 2. Population densities of species representing at least 1% of all animals collected in the survey of ten beaches occupied by sand dollar beds. False Bay values were not used to calculate the 1%. Values given are the pooled counts of three 0.01-m^2 samples. Abbreviations of sample locations are explained in Figure 2. # indicates tube builders.

a. Inside *Dendraster* Beds

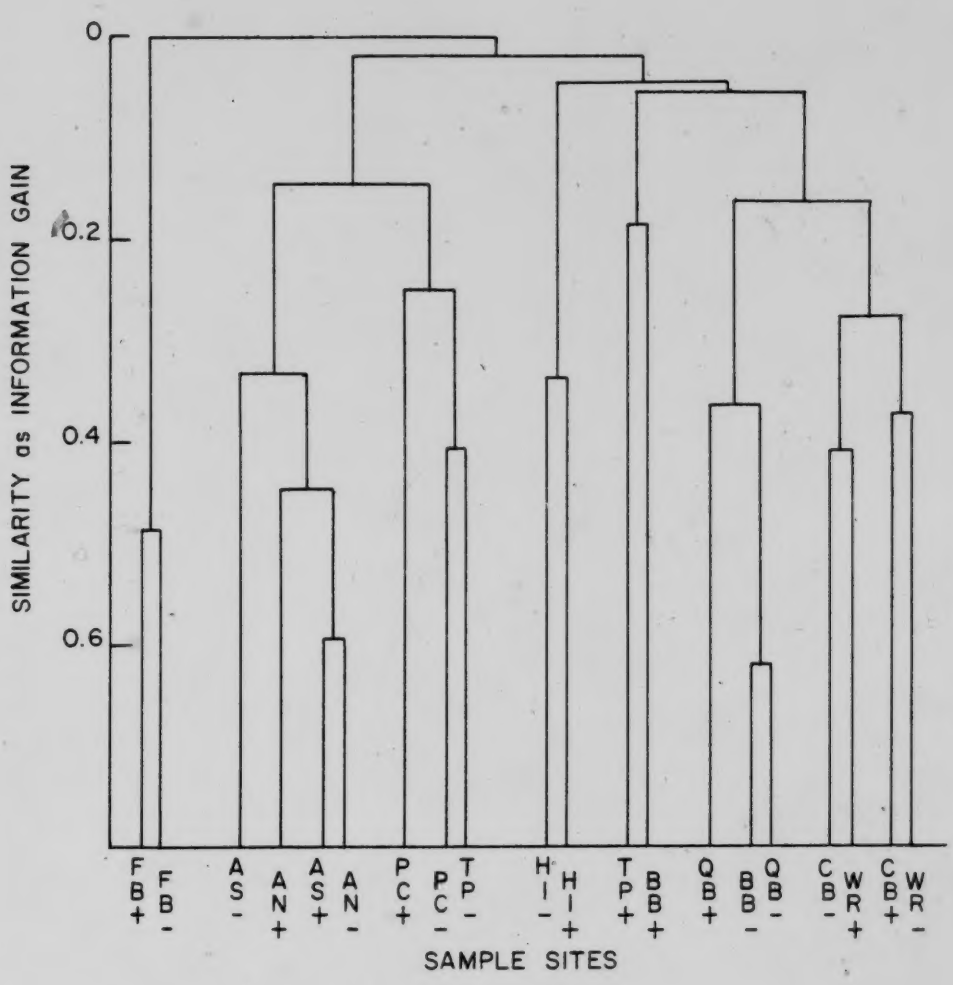
Species	Locations									
	TP	PC	AS	AN	BB	FB	WR	CB	QB	HI
Transennella tantilla	0	0	9	2	0	31	0	0	4	0
Mysella tumida	3	3	1	2	303	1	2	0	1	0
Opistobranch(juvenile)	0	0	2	0	0	0	2	1	0	0
Cumella vulgaris	15	1	39	1	13	1588	0	1	0	0
Lamprops quadriplicata	0	0	0	0	0	0	2	34	9	0
Paraphoxus spinosus	0	0	17	2	0	3254	0	0	0	0
Pontogeneia sp.	0	0	1	0	1	35	0	0	0	0
Anisogammarus confervicolus	0	0	4	0	0	1444	0	0	0	0
Anisogammarus pugettensis	1	0	0	1	0	0	0	6	0	0
Synchelidium shoemakeri	0	0	45	16	0	16	1	108	0	1
Euhaustorius washingtonianus	0	0	0	0	0	0	0	75	0	0
Corophium spp.#	0	0	4	0	0	1	0	2	0	0
Ampelisca agassizi#	0	0	0	0	0	0	0	0	0	0
Leptochelia savignyi#	0	0	26	0	1	29	0	0	0	0
Nephthys caeca	0	0	1	0	1	0	6	3	4	0
Scoloplos armiger	9	10	0	3	10	0	9	75	22	3
Glycinde polygnatha	2	5	23	7	1	0	2	0	0	0
Paronella? sp.	0	0	0	8	0	0	7	11	2	27
Armandia brevis	2	1	2	8	59	0	0	0	0	0
Malacoceros fulginosus#	0	0	0	0	0	41	0	0	0	0
Malacoceros arenicola#	0	0	2	0	0	0	0	0	0	0
Microspio sp.#	0	0	0	0	0	136	0	0	0	0
Pygospio elegans?#	0	0	0	0	0	0	24	0	0	0
Syllis heterochaeta?	0	0	0	0	0	0	0	162	2	1
Leptosynapta clarki	0	0	1	0	0	360	0	0	0	0

Table 2. Continued

b. Outside *Dendraster* Beds

Species	Locations									
	TP	PC	AS	AN	BB	FB	WR	CB	QB	HI
Transennella tantilla	0	0	26	27	5	126	0	0	4	0
Mysella tumida	6	4	3	0	8	7	0	0	4	0
Opistobranch(juvenile)	32	4	0	2	0	0	0	1	0	0
Cumella vulgaris	34	5	167	2	8	928	0	42	0	0
Lamprops quadriplicata	0	0	0	0	2	0	2	0	18	10
Paraphoxus spinosus	0	0	4	4	0	1024	0	0	0	0
Pontogeneia sp.	0	0	5	1	0	106	0	0	0	0
Anisogammarus confervicolus	0	0	1	0	0	9	0	0	0	0
Anisogammarus pugettensis	3	0	0	0	0	0	0	44	0	0
Synchelidium shoemakeri	1	0	108	10	2	251	1	2	0	0
Euhaustorius washingtonianus	0	0	0	0	0	0	0	6	0	0
Corophium spp.#	10	28	67	0	11	0	0	119	0	0
Ampelisca agassizi#	0	3	0	0	166	0	0	0	1	0
Leptochelia savignyi#	0	0	98	0	1	752	0	3	0	0
Nephthys caeca	0	0	0	1	6	0	1	4	3	1
Scoloplos armiger	11	5	1	3	11	0	13	67	20	1
Glycinde polygnatha	20	16	38	11	12	0	1	0	0	2
Paronella? sp.	1	0	0	10	0	0	0	10	7	57
Armandia brevis	0	0	0	6	2	2	0	0	0	0
Malacoceros fulginosus#	0	0	0	0	0	313	0	0	0	0
Malacoceros arenicola#	0	0	9	3	24	0	0	10	18	0
Microspio sp.#	0	0	0	0	0	19	0	0	0	0
Pygospio elegans?#	0	0	0	0	0	0	11	0	0	0
Syllis heterochaeta?	0	0	0	0	0	0	0	18	0	0
Leptosynapta clarki	0	0	0	0	0	84	0	0	0	0

Figure 3. Clusters of sampling sites based on faunal similarity. Similarity is measured as information gain based on the Shannon information content. Site abbreviations are explained in Figure 2.


0
0.2
0.4
0.6
SIMILARITY as INFORMATION GAIN
FB+
FB-
AS-
AN+
AS+
AN-
PC+
PC-
TP-
HI-
HI+
TP+
BB+
QB+
BB-
QB-
CB-
WR+
CB+
WR-
SAMPLE SITES

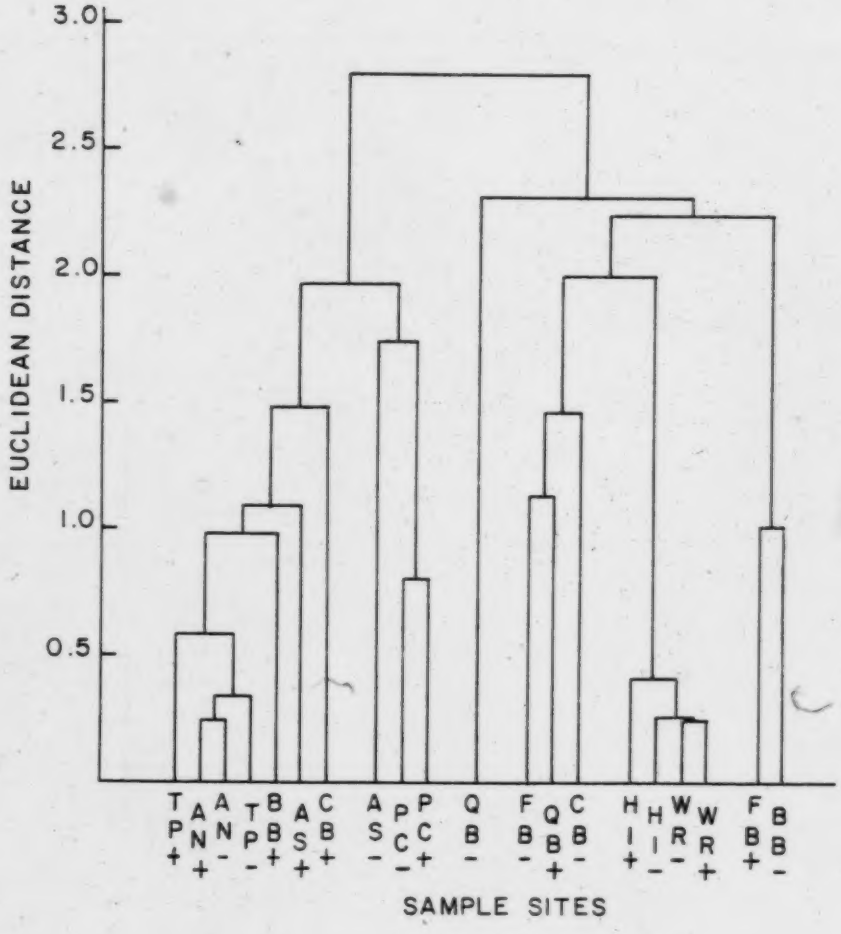
beaches on Puget Sound and the remaining beaches farther north. Only the sand dollar bed sample at Tolmie State Park appears misplaced by this division. The "inside" and "outside" samples from the same beach are not always most closely related to each other, but samples from adjacent beaches (Alki South and Alki North, Crescent Beach and White Rock) are grouped together.

The cluster of sites based on their sediment characteristics (Figure 4) follows a pattern similar, but not identical to, that of the faunal data. The division into two major groups separates the Puget Sound beaches from the other areas, with the Buck Bay and Crescent Beach sand dollar beds being included in the former group. The False Bay sediments do not differ notably from those of the other beaches. The clustering does not suggest a sediment composition typical of sand dollar beds, nor do any of the individual sediment characteristics measured show any relation to the presence or absence of Dendraster (Table 1).

The chi-square analysis indicates that no species encountered is significantly ($P<0.05$) either positively or negatively associated with Dendraster. This test fails to show associations apparently because most species are absent from both the sand dollar beds and the outside patches on several of the beaches, and species which are widespread occur in both habitats.

The absence of species from some beaches and the high variation among beaches makes it difficult to test species

Figure 4. Clusters of sampling sites based on sediment characteristics. Site abbreviations are explained in Figure 2.


3.0
2.5
2.0
1.5
1.0
0.5
EUCLIDEAN DISTANCE
TP+
AN+
AN-
TP-
BB+
AS+
CB+
AS-
PC-
PC+
QB-
FB-
QB+
CB-
HI+
HI-
WR-
WR+
FB+
BB-
SAMPLE SITES

abundances statistically. However, analyses of variance show that several species are significantly ($P<0.01$) more abundant outside the sand dollar beds, while one species is more numerous inside the beds. Species more abundant outside the beds include the bivalve Transennella tantilla, the tubicolous crustaceans Corophium spp., Ampelisca agassizi, and Leptochelia savignyi, and the polychaetes Glycinde polygnatha and Malacoceros arenicola, while the polychaete Armandia brevis is more numerous among the Dendraster. The amphipod Paraphoxus spinosus, which was found on only three of the beaches sampled, is more numerous inside than outside the sand dollar beds at the two sites where it is abundant, but this difference is not statistically significant ($P=0.09$). Among-beach inconsistencies in the distributions of the species tested are indicated, as in all cases the site X Dendraster-effect interactions are significant ($P<0.05$).

The Shannon-Weaver diversity, equitability and the number of species encountered are not significantly different inside and outside sand dollar beds. However, the diversity and number of species are lower inside than outside the beds at all sites except White Rock and Alki South (Table 3).

Analysis of variance showed no difference in the density of motile crustaceans inside and outside the sand dollar beds, although the density of crustaceans was significantly different among beaches, and the interaction

Table 3. Species diversity characteristics inside (+) and outside (-) ten sand dollar beds.

Location		Diversity (H')	Equitability	# of Species	# of Individuals
Tolmie State Park	+	2.6595	0.7689	11	50
	-	3.1151	0.8183	14	151
Puget City	+	2.4352	0.8119	8	24
	-	3.0943	0.7737	16	81
Alki South	+	3.4328	0.7142	28	194
	-	2.8962	0.6595	21	556
Alki North	+	3.3072	0.8467	15	59
	-	3.7469	0.8404	22	106
Buck Bay	+	1.3403	0.3215	18	401
	-	2.9166	0.6362	24	331
False Bay	+	2.1087	0.4663	23	7053
	-	2.7567	0.5799	27	3702
White Rock	+	3.4021	0.8010	19	70
	-	1.9679	0.7011	7	30
Crescent Beach	+	2.8180	0.6417	21	515
	-	2.9316	0.6482	23	342
Qualicum Beach	+	3.0593	0.8037	14	63
	-	3.2555	0.8334	15	93
Hornby Island	+	1.2680	0.4906	6	35
	-	1.5816	0.4990	9	80

was significant due to the large numbers of crustaceans in the sand dollar beds at False Bay and Crescent Beach. The density of tube builders was significantly ($P<0.05$) lower inside than outside the beds. The overall density of tube builders varied significantly among beaches. The interaction was significant because more tube builders were encountered inside than outside the Dendraster bed at White Rock (Table 4).

D. Discussion

Only one previous study has attempted to enumerate the fauna associated with Dendraster. Merrill and Hobson (1970) found no animals endemic to the subtidal, outer coast sand dollar beds of southern California, but they listed species which were recurrent in and characteristic of the beds. Most of the species more numerous inside than outside the beds were fish or crustaceans, including an amphipod of the genus Paraphoxus. The investigators felt that some organisms occurred with Dendraster because the sand dollars stabilized the substrate by curtailing the erosion of sand and also provided shelter from predators.

The results of the present study only partially concur with those of Merrill and Hobson. I found no species which seemed characteristic of sand dollar beds, but the polychaete Armandia brevis was significantly more numerous in the beds than in adjacent areas (Table 2). The amphipod

Table 4. A comparison of tube builder and motile crustacean population densities inside and outside sand dollar beds of varying densities. Sand dollar counts are given as means and standard errors of adults/0.25m^2. Tube builder and crustacean densities are givenas means and standard errors of animals/0.01m^2.

Location	Sand dollars	Tube Builders	Motile Crustaceans
Tolmie State Park	32.8± 5.9	0	6.0± 2.5
	0	4.7± 3.3	12.7± 3.8
Puget City	123.6±29.2	0	0.7± 0.3
	0	11.0± 6.4	3.0± 1.0
Alki South	93.2± 9.4	13.0± 7.5	36.0± 7.1
	0	63.0± 14.8	97.3± 17.8
Alki North	36.2± 5.5	1.0± 1.0	6.0± 2.3
	0	6.3± 2.3	6.0± 2.6
Buck Bay	59.4±10.9	1.3± 0.7	5.3± 0.7
	0	87.0± 53.6	5.0± 1.2
False Bay	2.7± 0.4	76.3± 31.0	2121.7±642.3
	0	394.7±149.0	782.0±353.1
White Rock	1.0± 0.4	11.0± 2.6	1.0± 0.6
	0	3.7± 2.2	1.3± 0.3
Crescent Beach	4.8± 1.4	5.3± 0.9	81.0± 13.2
	0	45.3± 14.2	32.0± 6.1
Qualicum Beach	21.4± 6.0	1.0± 0.6	3.3± 0.7
	0	8.0± 3.5	6.0± 1.0
Hornby Island	41.0±10.8	0	1.3± 0.6
	0	1.0± 1.0	4.3± 0.3

Paraphoxus spinosus was more numerous (although not significantly so) in the beds on the two beaches where it was abundant. The total number of crustaceans encountered (excluding tubicolous forms) was not greater in the beds than in the adjacent substrate at most of the beaches (Table 4).

The reason for the difference between these results and the observations of Merrill and Hobson is largely that I sampled intertidal rather than subtidal sand dollar beds. Since the sampling was done at low tide, fish and possibly motile crustaceans which might take refuge among submerged and inclined Dendraster could not be present. In addition, intertidal sand dollars, which burrow at low tide and incline at high tide must do more to destabilize the sediment than to stabilize it.

The total number of tube-building organisms was significantly ($P<0.05$) lower in the Dendraster beds than in the adjacent sand (Table 4). Although no species which occurred on the beaches sampled was consistently absent from the beds, six species, including four tubicolous crustaceans and polychaetes, were more abundant outside than inside the beds (Table 2). Since the repeated burrowing and inclining of intertidal sand dollars must frequently overturn the sediment, sedentary tube-building organisms should find it difficult to coexist with Dendraster.

At White Rock more tube builders were collected near the sand dollars than away from them. However, at this

location the Dendraster population was only 4 individuals/m^2, the lowest density encountered at any site. Such a sparse population apparently has no adverse effect on tube-building organisms.

Diversity, equitability and the number of species present were not significantly different inside and outside the sand dollar beds. Since the total number of animals collected at some of the sites was low, the validity of the t-statistic for comparing diversities is questionable (Hutcheson 1970), and attempts to base any conclusions on the diversity values are risky. However, diversities and numbers of species present were lower inside than outside the beds at all sites except White Rock, where the Dendraster population is probably too low to have any effect on diversity, and at Alki South (Table 3). Thus, there is some suggestion that fewer species are able to coexist with Dendraster, resulting in lower species diversities in sand dollar beds.

Fewer species have been encountered in areas disturbed by rays, crabs and moon snails than in undisturbed sites (Orth 1977, Virnstein 1977, Woodin 1978, Wiltse 1977). Wiltse (1977) attributed the lower diversities in snail enclosures to the loss of small tube-building polychaetes, particularly spionids. Similarly, exclusion of tubicolous polychaetes (including the spionid Malacoceros arenicola) may reduce the diversity of infauna in sand dollar beds.

This study thus suggests that although no recognizible

"sand dollar bed community" exists, several species, as well as tube-building organisms in general, are encountered less frequently in sand dollar beds than elsewhere. In a later chapter, I shall test the hypothesis that these types of organisms are excluded by Dendraster.

In addition to suggesting the relationship of Dendraster and the infauna, this study provides some information about the intertidal sand community of the protected coast of Washington and British Columbia. My observation of the widespread occurrence of Mysella tumida, Cumella vulgaris, Scoloplos armiger, Glycinde polygnatha, Nephthys caeca, Malacoceros arenicola, and Corophium spp. confirms the reports of Wieser (1959), Levings and Coustalin (1975) and Armstrong et al. (1976).

Cluster analysis (Figure 3) suggests that the faunal associations of the Puget Sound beaches are somewhat different from those of the other areas. The cluster of beaches by their sediment characteristics (Figure 4) follows a similar pattern, but sediment alone does not explain faunal distributions. Adjacent beaches (Alki South/Alki North and Crescent Beach/White Rock) have most similar fauna, but their sediments may have different characteristics. For example, the sediment of White Rock is most similar to that of Hornby Island. Water circulation inside and outside of Puget Sound, which must control the distribution of planktonic larvae and perhaps the dispersal of adults, is probably an important influence on community

composition.

The False Bay community differs substantially from the other associations sampled, having both a greater density of infauna and species not encountered elsewhere. Nothing which I measured can adequately explain this difference. Higher organic content of the sediment might account for greater faunal density, but although the percent organic carbon inside the sand dollar bed is higher at False Bay than at any other site, the organic content outside the bed is lower than that observed at many other locations (Table 1).

It was not the primary aim of this study to determine the distribution of infaunal communities, and the sampling pattern employed is inadequate to provide an accurate picture. While the sample size was large enough to represent the dense infauna of False Bay, it was too small for the sparse populations of White Rock, Hornby Island, and Puget City. More important, sampling only a limited area of each beach can miss even dominant species whose distribution is patchy. For example, on many of the beaches I observed mats of tubes above the sand dollar beds, often located on the tops of sand bars rather than in the troughs between, so that only minor differences in elevation apparently influenced the distribution of species. I took one core from each of these patches, although the data is not included in Table 2. At White Rock, where no Corophium were encountered in any of the primary samples, 908 of these amphipods appeared in the single core collected above the Dendraster

bed. Thus, although I have provided some quantitative information on the intertidal infauna of the northwest, any serious survey of these communities must include a series of sampling stations at each beach to characterize a fauna whose distribution shows marked patchiness.

III. Seasonal Changes in the Benthic Community of False Bay, San Juan Island, Washington, with Emphasis on the Role of the Sand Dollar Bed

A. Introduction

Large organisms which rework the sediment or alter its stability may play key roles in structuring soft-bottom communities (Rhoads and Young 1971, Woodin 1978). The Pacific sand dollar, Dendraster excentricus, reworks (sensu Rhoads 1967) at least the top 4cm of sediment (Chapter IV) and has been shown experimentally to limit the distribution of several infaunal species, particularly tubicolous forms (Chapter IV).

Although sampling data (Merrill and Hobson 1970; Chapter II) indicates that there are no animal species endemic to sand dollar beds, Merrill and Hobson have found that several species are more abundant in subtidal sand dollar beds than in adjacent areas without Dendraster, and I have demonstrated (Chapter II) that several species and tube-building animals in general are less numerous in intertidal sand dollar beds than in adjacent patches. Since the suite of species which occurs on different beaches shows considerable variation (Chapter II), relationships of individual species to Dendraster are difficult to demonstrate. However, the changes in infaunal population densities inside and outside the sand dollar bed on one beach might provide more useful suggestions about

interactions between a constant set of infaunal species and Dendraster.

Some researchers have followed temporal changes in sand-bottom communities which include Dendraster, but these studies have been confined to epifauna or to large (>3.2mm) infauna and have not related fluctuations in macrofaunal densities to changes in sand dollar populations or distributions. Fager (1968) monitored nine epifaunal species in the shallow subtidal and found that their populations remained relatively constant for six years. Davis and Van Blaricom (1978) followed up Fager's work and contradicted his observation of long term numerical stability, noting that populations of seven of the species, including Dendraster, had changed significantly. Peterson (1975) compared the stability of individual species and community composition in two California lagoons over 37 months and related fluctuations in the populations of individual species, including numbers of Dendraster, in part, to weather conditions.

I chose to study the intertidal sand flat at False Bay, San Juan Island, Washington. Although the sand dollar population there was relatively sparse (Chapter II), this site was selected because the bay is owned by the University of Washington and thus is protected from the disturbance of heavy public usage.

Some information about the fauna of False Bay is already available. Shelford et al. (1935) first sampled at

False Bay, describing the community as a Dendraster fasciation on a Macoma-Leptosynapta association. Pamatmat (1966, 1968) conducted a two-year study of the False Bay community, measuring monthly changes in numbers and biomass of the dominant species at three stations representing three tidal heights, but he was primarily interested in productivity rather than in explaining the spatial structure of the community, and few of his samples included Dendraster.

The following study consists of seasonal samples collected over two years at locations inside and outside the False Bay sand dollar bed. Spatial and temporal changes in the community and in the populations of individual species are evaluated in relation to the presence and absence of Dendraster. The sampling stations cover a limited tidal range so that among-site differences in faunal composition will be more likely to reflect species interactions than environmental differences.

B. Methods and Materials

The Study Site

The sand flat at False Bay is roughly circular and occupies an area of about 1.3km^2. It is approximately 500m wide at the mouth. From the mouth to the head of the bay extend a series of sand bars which Pamatmat (1966, 1968) has described as "quasi-permanent."

A small stream flows from the San Juan Valley and empties into the bay. Its freshwater discharge peaks during the winter and becomes negligible during the summer when the water is used for irrigation in the valley. The maximum input of freshwater into the bay which I observed occurred during heavy rains in December, 1975, when the stream's current was apparent almost to the mouth of the bay.

A more detailed description of False Bay is given by Pamatmat (1966, 1968).

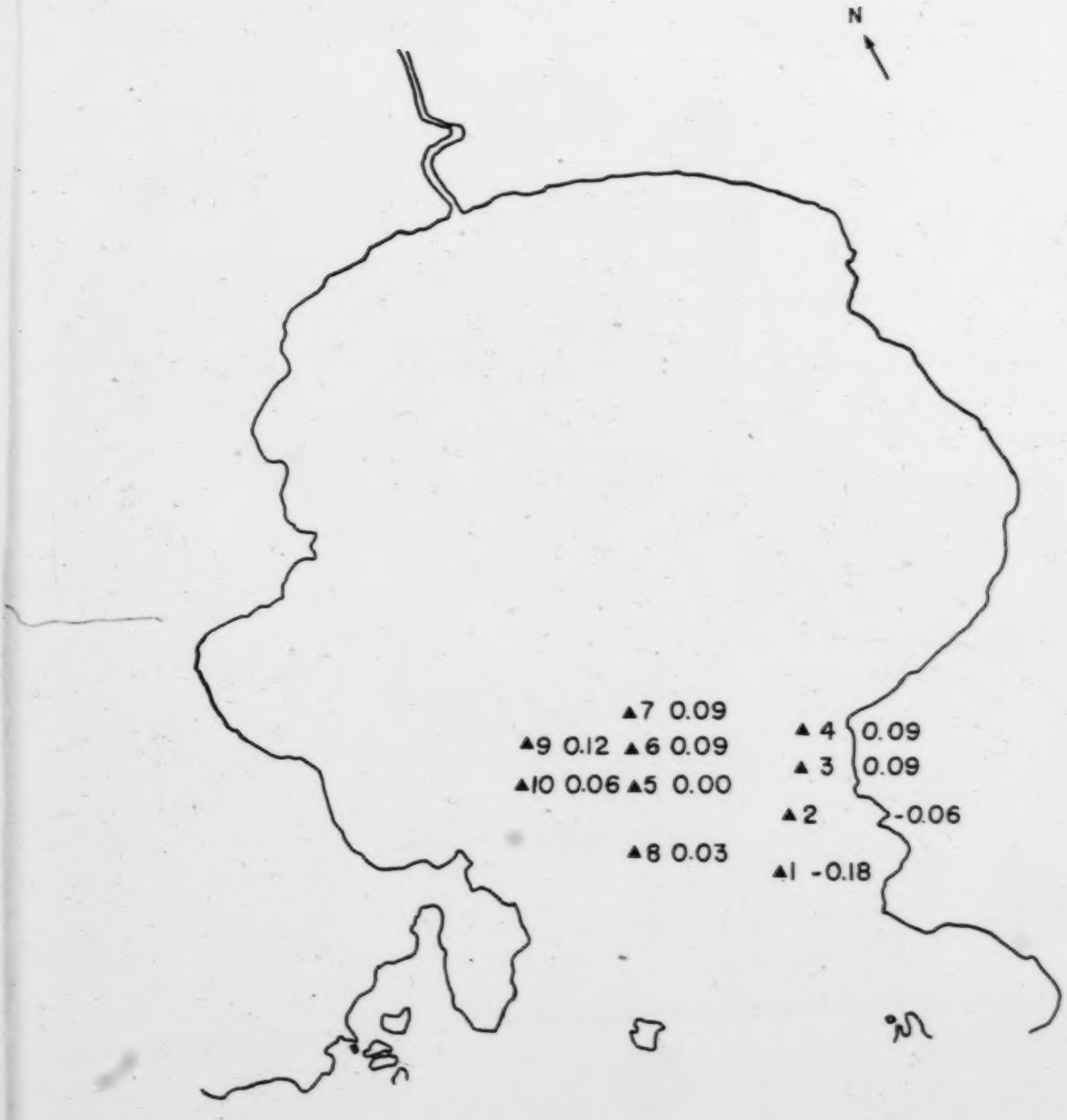
Ten stations were chosen in the troughs between sand bars near the mouth of the bay (Figure 5). Each site was marked with a wooden stake. The tidal height of each station was measured with a level.

Stations 1-4 were located in the sand dollar bed. Sand dollars also occurred in the eelgrass between stations 5 and 10 and were observed occasionally at all sites, but they remained continuously only in the troughs associated with stations 1-4.

Sampling Procedure

Each station was sampled four times a year for two years, in December, 1975; April, July and October, 1976; and January, May, July and October, 1977. Two replicate 0.01-m^2 cores were collected at each time. All samples were taken at random locations within a 1.0-m radius of the stake. The methods of sample collection, preservation and analysis were as described in Chapter II.

Figure 5. Map of False Bay, showing locations of sampling stations and their elevations (in meters) relative to MLLW (modified from Pamatmat 1968).


N
▲7 0.09
▲9 0.12 ▲6 0.09
▲10 0.06 ▲5 0.00
▲8 0.03
▲4 0.09
▲3 0.09
▲2 -0.06
▲1 -0.18

Densities of adult Dendraster in the troughs near stations 1, 2 and 3 were measured in April, 1975. Densities were estimated by counting all sand dollars present to a depth of 10cm in a 1.0-m^2 quadrat. Ten quadrats, placed at random, were counted at each station. The procedure was repeated in June, 1976, at stations 1, 2, 3 and 4. Sand dollar density at station 2 in June, 1977, was estimated from the quadrats used to study movement. (See Chapter IV.)

Sediment Analysis

One additional sample was collected at each time for sediment analysis. Sediment was collected with a trowel to a depth of 10cm and analyzed for organic carbon, mean grain size and sorting coefficient as described in Chapter II.

Differences in organic content, grain size and sorting coefficient among sampling sites and times were tested with analysis of variance followed by Student-Newman-Keuls multiple range tests and partitioning the among-sites sums of squares into Dendraster-bed vs. "outside" stations comparisons (Snedecor and Cochran 1967). Only the December, 1975; April, 1976; and July, 1977, samples were tested for grain size and sorting differences. All dates except December, 1975, and May, 1977, were analyzed for differences in organic carbon content.

Statistical Analysis of Faunal Data

Species were ranked by abundance (Fager, 1957;

Virnstein, 1977) at each station and for each sampling period. The most abundant species in the two replicates at a sampling site received 10 points, the next most abundant nine points, etc. Points received at each sampling period were totalled to determine the dominant species at each location (1). Similarly, species were ranked by abundance (totalled over all 10 stations) for each of the eight sampling times (2). Thus, 80 points was the maximum possible for dominance at a station (1) or for overall dominance (2). Alternatively, overall dominance was calculated by totalling the points each species received at each station for all sampling periods (i. e., the sum of all points a species received in calculation 1), providing a maximum score of 800 (3).

Information about the organisms' distributions can be obtained from the different methods of abundance ranking. Among-site variations in the rankings of a given species (calculation 1) may suggest patchiness in that organism's distribution. Similarly, for any species, lower ranking by calculation 3 than by calculation 2 implies a patchy distribution.

Spatial and temporal variations in densities of the eleven most abundant species (based on total number of individuals observed in all 160 samples) were analyzed further. Three-way factorial analyses of variance followed by multiple range tests were used to test annual, seasonal and among-station differences. The population densities of

each species inside and outside the sand dollar bed (stations 1-4 v. 5-10) were compared by partitioning the among-stations sums of squares (Snedecor and Cochran 1967). The replicate samples, with densities transformed using ln (x+1), were used for these calculations.

Analysis of variance was also used to compare densities of sand dollars from year to year and among stations.

Multivariate Statistics

Three types of multivariate analyses were used to identify structure in the False Bay community. Thirty-five species which were collected during at least half of the eight sampling times were used for these analyses. The abundance of each species was calculated as its mean density in the two replicate cores. The abundances were normalized using the log(x+1) transformation for principal component and discriminant analyses, while untransformed abundances were used for cluster analysis.

Cluster analysis is a classification technique which groups together samples which contain similar fauna. For the False Bay data it was used to detect possible spatial or temporal patterns in the faunal assemblage. The 80 station-time combinations were clustered using BMDP:2M (revised December, 1977) of the BMDP statistical package (Dixon and Brown 1977). The distance between sites was measured as the chi-square statistic for the equality of two sets of frequencies, where the frequencies are counts of

individuals representing each species encountered. This method puts little weight on the difference between zero and one of a species encountered in a sample pair. It is, therefore, more appropriate than the information statistic used in Chapter II for evaluating the False Bay data, where the difference between zero and one of any species at a sampling station is probably due to chance.

Principal component analysis reduces the information contained in a matrix of species correlations or covariances to vectors, a small number of which account for most of the variation. The elements of each vector (coefficients or factor loadings) give the weighting of each species in the component. High weightings and coefficients with like signs have been used to define species associations which represent communities (Cassie and Michael 1968). The components have also been used to suggest hypotheses about the causes of variation in a system (Sprules 1977).

I have based the principal component analysis of the False Bay data on the covariance matrix. This method emphasizes the numerically dominant species, which are the only organisms about which hypotheses can later be tested experimentally.

While principal component analysis is an a posteriori statistical procedure used to search for structure in faunal data, discriminant analysis is an a priori statistical procedure which assesses differences among pre-defined groups. Discriminant analysis provides canonical variables

which are vectors whose elements are the coefficients of the species which contribute to the maximum separation of the groups. These coefficients do not, however, represent the relative contribution of each species as do the factor loadings of principal component analysis (Cassie and Michael 1968). The stepwise discriminant analysis successively tests each species to determine which ones contribute significantly to the separation. It also provides a statistical test of significance of the separation of the groups.

I divided the 80 samples into four groups for discriminant analysis. The first division separated the stations in the sand dollar bed from those outside the bed. The second division was based on season, separating fall and winter samples from spring and summer samples. This grouping was chosen because Pamatmat (1966, 1968) had reported that populations of most of the dominant species in False Bay increased in spring and summer and decreased in fall and winter. Thus, group 1 encompassed the samples taken from the sand dollar bed in fall and winter, group 2 the sand dollar bed in spring and summer, group 3 the remaining stations in fall and winter, and group 4 the remaining stations in spring and summer.

Discriminant analysis has been used to ordinate ecological data. Green (1971) used species to define groups and calculated the discriminant functions (canonical variables) from measurements of environmental parameters.

Bernstein et al. (1978) calculated discriminant functions from environmental measurements, which included biotic as well as physical factors, but obtained their groups from classification statistics. I have based my groups on environmental factors (space and time) and calculated the discriminant analysis from species abundances.

The multivariate analyses were done using computer programs BMDP:2M, 4M, and 7M (revised December, 1977) (Dixon and Brown 1977).

C. Results

Tide Levels

The maximum difference in tidal heights among stations was one foot, with station 1 being 0.3m lower than station 9 (Figure 5). Station 1 was 0.12m lower than the next lowest site, station 2. Stations 3 and 4 were not lower than the sites outside the sand dollar bed.

The Sediments

The organic content of the sediments was lower in the 1977 samples than in the 1976 samples (Table 5), but the studentized range test showed that only the October, 1976, and July, 1977, samples were significantly different from each other. No clear seasonal patterns were detectible. The differences among sampling stations were significant at the 1% level, and the organic carbon content was significantly

Table 5. Organic contents (expressed as percentages) at ten stations in False Bay. Values given are means of two analytical replicates.

	Date					
Station	3/76	7/76	10/76	1/77	7/77	10/77
1	0.73	0.68	0.79	0.51	0.43	0.53
2	0.70	0.72	0.68	0.56	0.60	0.89
3	0.70	0.71	0.92	0.64	0.59	0.75
4	0.66	0.72	0.75	0.54	0.38	0.47
5	0.62	0.58	0.60	0.56	0.47	0.48
6	0.48	0.64	0.67	0.73	0.56	0.48
7	0.60	0.70	0.68	0.54	0.37	0.37
8	0.59	0.69	0.88	0.36	0.33	0.47
9	0.69	0.77	0.59	0.72	0.60	0.62
10	0.69	0.60	0.65	0.57	0.54	0.57

higher ($P<0.01$) inside than outside the sand dollar bed.

Mean grain size varied significantly among sampling stations ($P<0.01$). The coarsest sand was found at station 8, where the mean grain size was 2.1 phi (Table 6), while the finest, 2.5 phi, occurred at stations 2, 3 and 4. The sediment inside the Dendraster bed was significantly ($P<0.01$) finer than that outside the bed.

The sorting coefficient also varied significantly ($P<0.01$) among sampling stations, with the sediment inside the Dendraster bed being better sorted than that outside the bed. significant ($P<0.01$), with the December, 1975, samples being less well sorted than the April, 1976, or July, 1977, samples.

The Dominant Species

The population of Dendraster showed some annual and among-site fluctuations (Table 7). In 1975, the densities of sand dollars at stations 1, 2 and 3 were not significantly different. The 95% confidence interval for the population of Dendraster at all stations was 9.3 ± 2.5 animals/m^2. In 1976, the mean numbers of Dendraster at stations 2 and 4 (8.2 and 9.9/m^2, respectively) were similar to densities measured the previous year, but the densities at stations 1 and 3 (3.6 and 4.6/m^2, respectively) were significantly ($P<0.05$) lower. No environmental differences were observed which could account for these variations in sand dollar densities.

The False Bay infaunal community was characterized by

Table 6. Sediment mean grain size and sorting coefficients at the ten stations in False Bay. Values are given in phi units.

Station	Date	Mean Grain Size	Sorting Coefficient
1	Dec., 1975	2.30	0.48
	April, 1976	2.42	0.40
	July, 1977	2.39	0.46
2	Dec., 1975	2.44	0.44
	April, 1976	2.49	0.38
	July, 1977	2.47	0.39
3	Dec., 1975	2.53	0.43
	April, 1976	2.50	0.40
	July, 1977	2.54	0.41
4	Dec., 1975	2.49	0.52
	April, 1976	2.51	0.43
	July, 1977	2.58	0.44
5	Dec., 1975	2.33	0.52
	April, 1976	2.35	0.44
	July, 1977	2.45	0.44
6	Dec., 1975	2.28	0.52
	April, 1976	2.27	0.49
	July, 1977	2.34	0.56
7	Dec., 1975	2.30	0.65
	April, 1976	2.29	0.62
	July, 1977	2.27	0.62
8	Dec., 1975	2.13	0.54
	April, 1976	2.09	0.48
	July, 1977	2.10	0.53
9	Dec., 1975	2.44	0.56
	April, 1976	2.33	0.51
	July, 1977	2.38	0.52
10	Dec., 1975	2.45	0.49
	April, 1976	2.37	0.51
	July, 1977	2.45	0.47

Table 7. Population densities of Dendraster excentricus at four stations in False Bay, 1975-76. Means are expressed as adults/m^2.

	1975		1976	
Station	Mean	Std. Dev.	Mean	Std. Dev.
1	10.6	6.8	3.6	1.8
2	9.7	9.1	8.2	4.2
3	7.7	3.2	4.6	2.5
4	-	-	9.9	6.3

numerical dominance of a few species. Four species, Paraphoxus spinosus, Leptochelia savignyi, Cumella vulgaris, and Malacoceros fulginosus made up 81.36% of all animals encountered during the two-year study. These species plus seven others, Anisogammarus confervicolus, Transennella tantilla, Leptosynapta clarki, Synchelidium shoemakeri, Pontogeneia sp., Microspio sp., and Eusyllis? represented 96.06% of all individuals observed. These 11 species were also the dominants when ranked by seasonal and season X station abundances (Table 8). The ranks of the dominant species varied among the sampling stations, and eight additional species emerged as local dominants (Table 9).

Some relevant biological characteristics of these species are summarized in Table 10.

The population densities of the dominant species showed both spatial and temporal fluctuations, which were reflected in the variations in their dominance rankings by the different methods of calculation (Table 8). Species which were present and relatively abundant at all times and all stations (P. spinosus, Leptosynapta) ranked as high or higher by seasonal and station X season abundances (calculations 2 and 3) as they did by total number encountered throughout the study. Species displaying strong seasonal abundance patterns (Cumella, Synchelidium) ranked lower by seasonal than by total abundance, while species with particularly patchy spatial distributions (Leptochelia, Malacoceros) ranked lower by the station X season

Table 8. Abundances of the dominant species in False Bay ranked by total number collected in 160 samples, by seasonal abundance (calculation 2), and by seasonal abundance at each of ten sampling stations (calculation 3).

Species	Total Abundance Rank	Seasonal Abundance Rank	Seasonal Abundance Score	Station X Season Rank	Station X Season Score
Paraphoxus spinosus	1	1	78	1	750
Leptochelia savignyi	2	2	68	4	389
Cumella vulgaris	3	4	43	2	485
Malacoceros fulginosus	4	3	53	5	349
Anisogammarus confervicolus	5	9	22	11	130
Transennella tantilla	6	6	31	6	287
Leptosynapta clarki	7	5	38	3	444
Synchelidium shoemakeri	8	7	24	10	184
Pontogeneia sp.	9	11	18	9	192
Microspio sp.	10	8	23	7	272
Eusyllis? sp.	11	10	19	8	197

Table 9. Rank abundances of the ten most abundant species at each station in False Bay. Rankings were calculated from eight samples taken over two years (calculation 1). R=Rank, S=Score

Species	Stations 1 R	1 S	2 R	2 S	3 R	3 S	4 R	4 S	5 R	5 S	6 R	6 S	7 R	7 S	8 R	8 S	9 R	9 S	10 R	10 S
Paraphoxus spinosus	1	80	1	80	1	80	1	75	1	67	1	76	2	65	1	80	1	70	1	77
Leptochelia					9	23	2	69	3	57	2	61	1	79			3	52	4	48
Malacoceros	9	24							2	64	4	54	3	63	6	30	1	70	5	44
Cumella	3	50	3	50	3	60	3	64	5	38	3	59	5	34	5	37	6	38	2	55
Leptosynapta	2	53	2	59	2	61	4	42	9	21	5	47	7	30	6	30	4	51	3	50
Transennella					8	25	9	19	5	38	6	42	4	45	6	30	4	51	6	37
Synchelidium	8	29	4	44	10	17	7	22							2	47			8	25
Microspio	7	34	8	19	7	28	8	20	8	22	7	23	9	20	2	47	7	26	7	33
Anisogammarus	5	41	6	33	6	29									9	27				
Eusyllis?					4	47	6	36	4	52			8	26			8	21	10	15
Pontogeneia	6	37	5	38	5	39	5	40			8	20							9	18
Lumbrineris									7	26			5	34			8	21		
Paraphoxus tridentatus	4	42	7	21							9	15			2	47				
Lysianassid	10	21													10	24				
Nebalia			9	18					10	12										
Nemertopsis													9	20			10	15		
Calliopius			10	17																
Protomedia							10	14												
Oligochaete											10	8								

Table 10. Biological characteristics of dominant False Bay infaunal species. Taxonomic information is given in parentheses. A=amphipod, B=bivalve, C=cumacean, H=holothurian, P=polychaete, T=tanaid. Information about reproduction was obtained from personal observation and from Pamatmat (1968). e=eggs observed in brood pouches or in tubes, j=juveniles in sediment.

Species	Adult Length (mm)	Lifestyle	Reproductive Season
Paraphoxus spinosus(A)	4	Burrower	e: All year
Leptochelia(T)	6	Tube builder	e: Mar.-Dec.
Malacoceros(P)	20	Tube builder	e: Apr.-May
Cumella(C)	3	Burrower	e: Mar.-Dec.
Leptosynapta(H)	80+	Semi-permanent burrow	j: Apr.-May
Transennella(B)	5	Epifaunal	j: May-July
Synchelidium(A)	4	Burrower	e: May-Jan.
Microspio(P)	25	Tube builder	j: May
Anisogammarus(A)	8	Epifaunal/burrower	e: May-Oct.
Eusyllis?(P)	5	Burrower	?
Pontogeneia(A)	12	Epifaunal	e: Apr.-Nov.
Lumbrineris(P)	90+	Semi-permanent burrow	j: Oct.-Apr.
Paraphoxus tridentatus(A)	6	Burrower	e: Jan.-June

calculation. Anisogammarus, whose occurrence was highly seasonal and which at its seasonal maximum was numerous at only a few stations (1,2,3,4 and 8) ranked much lower (ninth and eleventh, respectively) by seasonal and station X season abundances than by total number encountered (fifth).

Abundance rankings by station (calculation 1; Table 9) revealed some patterns of dominance which appeared related to the presence or absence of Dendraster. Anisogammarus, Synchelidium and Pontogeneia received their highest rankings at the sand dollar bed stations (1-4), although Anisogammarus and Synchelidium also ranked high at station 8. Leptosynapta ranked highest at stations 1, 2 and 3. Transennella, Leptochelia and Malacoceros ranked lowest at the Dendraster bed stations and highest at the "outside" stations, except that Leptochelia ranked second at station 4 and lower than tenth at station 8. The remaining species (P. spinosus, Cumella, Microspio and Eusyllis?) showed no patterns of abundance which corresponded with the presence or absence of sand dollars.

Analyses of variance showed significant ($P<0.01$) among-station differences in abundances of all species tested, and some of this variation could be related to the Dendraster bed. When the sums of squares for stations were partitioned into the portion due to the difference between the sand dollar bed and the "outside" stations and the portion due to within-assemblage variation, the difference between the sand dollar bed and the "outside" stations was

significant ($P<0.05$) for all species except Microspio and Eusyllis? (Table 11), but the within-assemblage variation was also significant for all species. The difference between the sand dollar bed and the "outside" stations accounted for 76.60% of the among-station variation for Pontogeneia, 70.75% for Malacoceros and 51.25% for Transennella, but it explained only 3.61% of the variation for Cumella and 8.98% of the variation for Leptosynapta.

Multiple range tests also suggested patterns of species abundances related to the sand dollar bed, but showed that densities of most species often varied significantly ($P<0.05$) between pairs of sampling stations within the sand dollar bed or within the "outside" group. P. spinosus, Anisogammarus, Synchelidium and Pontogeneia were all significantly more abundant at stations 1-4 (the sand dollar bed) than at most of the "outside" stations, although P. spinosus was also significantly more abundant at station 6, Anisogammarus more abundant at station 8, and Synchelidium more abundant at stations 8 and 10 than at the remaining "outside" stations. Leptochelia, Malacoceros and Transennella were all significantly less abundant in the sand dollar bed and at station 8 than at the outside stations, except that Leptochelia was very abundant at station 4. The abundance patterns of Cumella, Leptosynapta, Microspio and Eusyllis? were not clearly related to the presence or absence of Dendraster.

Large numbers of Leptochelia were collected at station

Table 11. A summary of the partitioning of the sums of squares for stations into between Dendraster-bed and other stations and within-assemblage components, giving the percentages of the sums of squares accounted for by the sand dollar bed comparison. Degrees of freedom for stations=9, between=1, within=8, MSE=80.

Species	Stations	Between	Within	%	MSE
P. spinosus	62.032	28.077	33.955	45.26	0.154
Leptochelia	525.323	93.790	431.533	17.85	0.285
Malacoceros	425.788	301.235	124.553	70.75	0.524
Cumella	86.439	3.119	83.320	3.61	0.221
Leptosynapta	50.832	4.566	46.266	8.98	0.189
Transennella	178.205	91.326	76.879	51.25	0.231
Synchelidium	83.612	20.119	63.493	24.06	0.319
Microspio	14.290	0.951	13.338	6.66	0.490
Anisogammarus	108.666	36.992	71.674	34.04	0.310
Eusyllis?	130.935	0.028	130.908	0.02	0.319
Pontogeneia	58.579	44.873	13.705	76.60	0.418

4 because that station was located on the edge of a tanaid bed. Sampling on the shoreward side of the marker stake collected high numbers of Leptochelia, while samples from the opposite side of the stake contained fewer tanaids. While the trough in which station 4 was located contained a large population of Dendraster (Table 7), I observed that the sand dollars appeared concentrated toward the center of the bay and away from the tanaids.

Population densities of the eleven species tested showed temporal fluctuations which included both annual and seasonal differences. Populations of all species except Anisogammarus were significantly ($P<0.05$) different in 1975-76 than in 1977. Numbers of all species varied seasonally, with order-of-magnitude differences between population maxima and minima for most species.

Multiple range tests for among-season differences in abundances revealed two basic patterns. Most species, including P. spinosus, Leptochelia, Malacoceros, Transennella and Eusyllis?, reached their peak abundances in the fall samples and were usually least abundant in the spring. Cumella, Anisogammarus, Synchelidium and Pontogeneia reached their peak abundances in the summer, and all but the last species almost disappeared from the bay in winter. Synchelidium populations remained elevated into the fall, but Cumella and Anisogammarus were numerous only in the summer samples. The other two species, Leptosynapta and Microspio, showed no clear abundance peaks, although their

juveniles were observed only in the spring samples.

The spatial and temporal patterns in distribution and dominance of the major False Bay species are summarized in Table 12.

For most species the station X season, station X year, season X year and three-way interactions were significant at least at the 5% level. These interactions are important because they suggest that not only were the spatial distributions of the species patchy, but that the locations of species' greatest densities did not remain constant.

Shifts in the locations of patches of Leptochelia were most dramatic. Following a maximum density at station 7 of 1548 tanaids/0.01m^2 in October, 1976, the population reached a seasonal maximum of only 454/0.01m^2 there in October, 1977, while at station 6 the population increased from a 1976 maximum of 84/0.01m^2 to 2541/0.01m^2 in October, 1977. Such shifts did not appear to be related to changes in the distribution of Dendraster.

The Community

Although the population densities of the dominant species varied seasonally and annually, the species composition of the community changed little during the two-year study. Of the 35 species used for multivariate analysis, 26, including all 11 of the dominants, were encountered at all sampling times. Only one species which appeared as a local dominant was absent at any sampling

Table 12. A summary of the spatial and temporal distributions of the False Bay species, based on dominance rankings (Table 9) and analyses of variance. Numbers refer to stations. Populations at stations of most abundance are significantly ($P<0.05$) different from populations at locations of least abundance.
* indicates remaining stations.

Species	Dominance		Seasonal		Abundance	
	High	Low	Maximum	Minimum	Most	Least
P. spinosus	All	--	Fall	Spring	1,2,3,4,6	*
Leptochelia	4,5,6,7,9	1,2,8	Fall	Spring	7	1,2,3,8
Malacoceros	5,6,7,9	2,3,4	Fall	W/Sp	5,7,9	1,2,3,4,8
Cumella	*	6	Summer	Winter	*	4,6
Leptosynapta	1,2,3	5	Not Clear		*	5,8
Transennella	5,6,7,8,9,10	1,2	Fall	Spring	5,6,7,9	*
Synchelidium	*	5,6,7,9	Su/F	W/Sp	*	5,6,7,9
Microspio	8	*	Not Clear		*	2
Anisogammarus	1,2,3,8	*	Summer	Winter	1,2,3,4,8	*
Eusyllis?	*	1,2,6,8	Fall	Rest	3,4,5,7,9	1,2,8
Pontogeneia	1,2,3,4	*	Summer	Rest	1,2,3,4	*

time: the amphipod Calliopius sp. was not encountered in May, 1977. Since the remaining species were relatively rare, their absence from the samples on any date probably did not indicate their absence from the bay.

Cluster analysis divided the 80 samples into five groups which roughly represent the sand dollar bed plus station 8 in fall and winter, the sand dollar bed plus station 8 in spring and summer, most other stations (5, 6, 9, 10) in spring and summer, most other stations in fall and winter, and high density tanaid beds (>300 Leptochelia/0.01m^2, except station 7 in April, 1976) (Figure 6). These groupings were not rigid, however. There was some overlap between the seasonal groups, and stations 6 and 10 from the December, 1975, sampling were included with the sand dollar bed. The samples from station 4 frequently were included in the "other stations" grouping, probably because of that station's location on the edge of a tanaid bed.

The cluster analysis suggests that the fauna of station 8 is more closely related to that of the sand dollar bed than to the other "outside" stations. This assumption is supported by the patterns of distribution of the dominant species. Leptochelia, Malacoceros and Transennella, which were rare in most of the sand dollar bed, were also rare at station 8, while Anisogammarus and Synchelidium, which were most abundant in the Dendraster bed, were also abundant at station 8 (Table 12).

Principal component analysis produces as many

Figure 6. Clusters of the 80 samples of False Bay infauna. The five major groups, identified by circled numbers, are as follows:

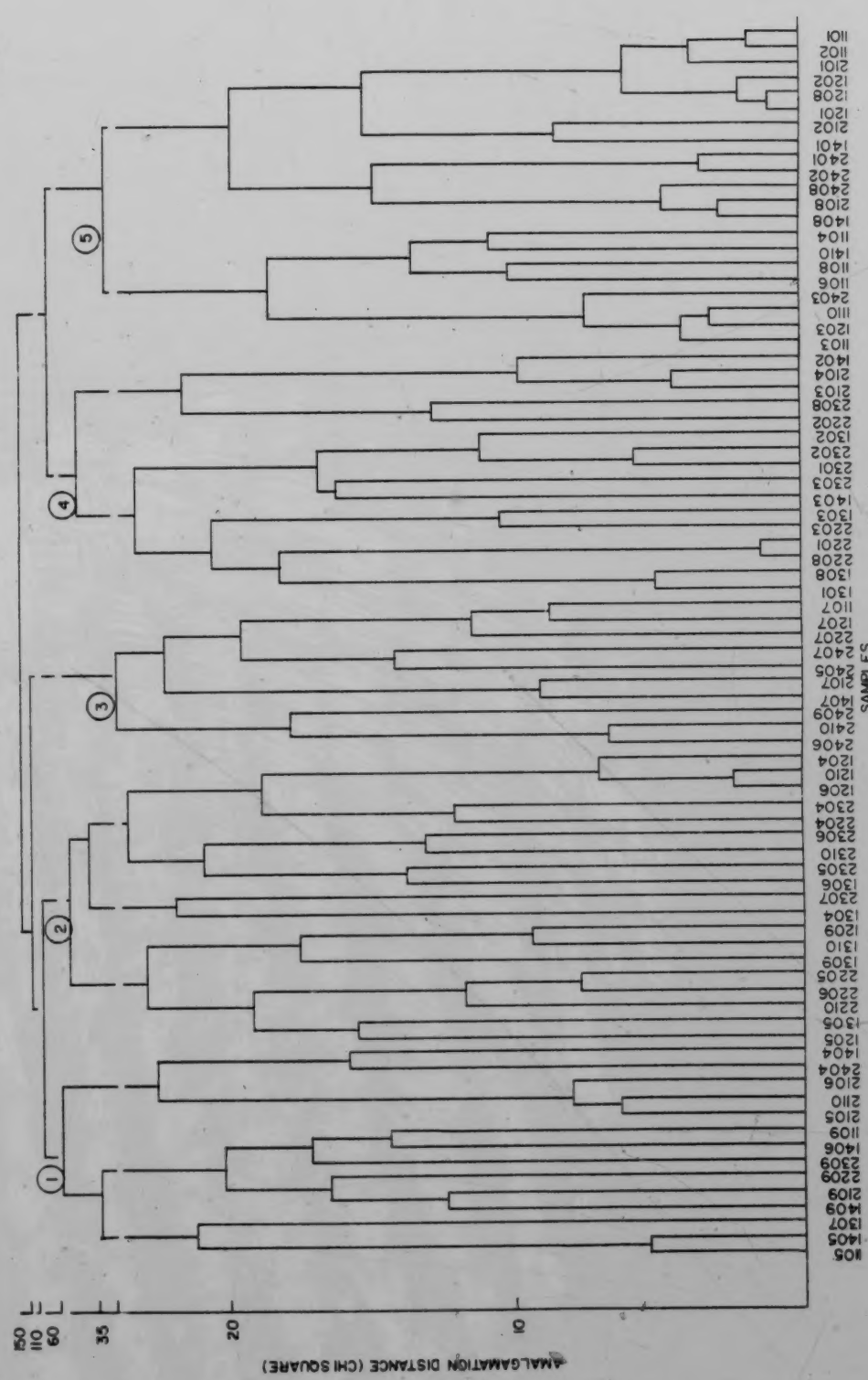
1- "Outside" stations in fall and winter
2- "Outside" stations in spring and summer
3- High density tanaid beds
4- Sand dollar bed in spring and summer
5- Sand dollar bed in fall and winter

Each sample is coded numerically as follows:

The first number represents the year.
1- 1975-76
2- 1977

The second number represents season.
1- Winter
2- Spring
3- Summer
4- Fall

The third number (two digits) represents the sampling station (1-10).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AMALGAMATION DISTANCE (CHI SQUARE)

components as there are variables (species). The significance of each of these components can be tested statistically, but it is more convenient to discuss only the components which can be interpreted reasonably than to include all components which might be statistically significant (Cassie and Michael 1968).

The principal component analysis of the False Bay data produced seven components which accounted for 79.8% of the total variance (Table 13). However, only three of these components can be usefully interpreted. The factor loadings of these three components are presented in Table 14. Following the method of Cassie and Michael (1968), the species are arranged in descending order of the elements of the first vector, and the highest absolute loading received by each species is indicated with an asterisk. Not all species have a coefficient marked with an asterisk, as for several species the highest loading was on a component not represented here.

According to Cassie and Michael, marked coefficients in the same vector which have like signs indicate species which are members of the same community. Since I sampled from a limited tidal range on a single beach, my samples should all have come from what is normally considered one community. Further, I studied temporal as well as spatial distributions. Thus, this type of interpretation is not entirely appropriate to my data, but it might separate a "sand dollar bed community" from an "outside" community.

Table 13. Percentages of the total variance in population densities of False Bay infauna explained by seven principal components.

Principal Component	Cumulative % of Total Variance
1	35.0
2	51.5
3	60.4
4	67.7
5	73.2
6	76.7
7	79.8

Table 14. Factor loadings on the first three principal components of 35 False Bay infaunal species. * indicates the highest absolute loading for a species. # indicates tube builders.

Variable (Species)	PC 1	PC 2	PC 3
Leptochelia savignyi#	0.7630*	0.0121	0.3930
Malacoceros fulginosus#	0.7350*	-0.1110	0.1210
Transennella tantilla	0.4710*	-0.0411	0.1310
Lumbrineris zonata	0.1850	-0.0352	0.2650*
Protomedia zotea?#	0.1660*	-0.0872	-0.0407
Axiothella rubrocincta#	0.1570*	-0.0126	-0.0020
Nemertopsis gracilis	0.1560*	-0.1370	0.1360
Mysella tumida	0.1250*	-0.0172	-0.0264
Photis brevipes#	0.1220*	-0.0170	-0.0403
Microspio sp.#	0.0957	0.0963	0.0217
Amphiporus sp.	0.0786*	-0.0083	0.0628
Phyllodocidae spp.	0.0765*	-0.0036	0.0447
Nebalia pugettensis	0.0574	0.0016	0.0564
Onuphis elegans#	0.0529	0.0650	0.0629
Other Nemerteans	0.0506*	-0.0100	0.0111
Leptosynapta clarki	0.0433	0.0654	-0.0380
Nereidae spp.#	0.0426	-0.0181	-0.0110
Eusyllis? sp.	0.0396	0.0380	0.3850*
Capitellidae spp.	0.0378	-0.0312	0.0673*
Armandia brevis	0.0364	-0.0945	0.1220*
Podoceropsis sp.#	0.0330	-0.0057	-0.0205
Oligochaetes	0.0325	-0.0256	0.1710*
Clinocardium nuttallii	0.0231*	-0.0079	0.0095
Macoma spp.	0.0097*	0.0031	0.0067
Cumella vulgaris	0.0042	0.3460	-0.0688
Paronella? sp.	-0.0035	-0.0122	-0.0303
Corophium insidiosum#	-0.0069	-0.0159	0.0069
Lamprops sp.	-0.0130	0.0348	0.0211
Paraphoxus spinosus	-0.0382	0.0697	-0.1250
Synchelidium shoemakeri	-0.0385	0.3800	-0.0532
Lysianassid amphipod	-0.0467	-0.0262	-0.1420
Paraphoxus tridentatus	-0.0506	0.0522	-0.2870*
Calliopius sp.	-0.0756	0.1400*	0.0037
Pontogeneia sp.	-0.1530	0.0478	0.0688
Anisogammarus confervicolus	-0.2440	0.6860*	-0.1350

Thirteen species have their highest absolute loadings (all positive) on the first principal component. These species are tubicolous polychaetes and crustaceans, bivalves and nemerteans, with the phyllodocids the only non-tubicolous polychaetes included. Nemerteans and phyllodocids are predators, and I have observed Nemertopsis gracilis feeding on Leptochelia in the laboratory. It is reasonable that these predators should be found among high densities of potential prey. Thus, principal component 1 represents an association of tube builders, their predators and small clams.

Dense concentrations of these tube builders do not occur in the sand dollar bed (except the Leptochelia at station 4, as previously noted). None of the species with negative coefficients in the first vector has its highest absolute loading on that factor, but most of the species with negative coefficients are epifaunal or burrowing amphipods which are most numerous in the Dendraster bed.

Only two species have their highest absolute loadings on principal component 2. Both are amphipods, Anisogammarus confervicolus and Calliopius sp., which are abundant only in the summer. Thus, this vector reflects a seasonal factor rather than a spatial "community".

Four of the five animals whose highest absolute coefficient occurs in principal component 3 are burrowing polychaetes, or at least polychaetes which do not possess obvious tubes, and may represent a burrowing polychaete

association which is separate from the association of tube builders as Woodin (1974, 1976) predicts. However, this group does not appear to be excluded by the tube builders, but rather is associated with some of the stations where Malacoceros and Leptochelia are most abundant.

The principal component analysis can be interpreted alternatively by considering the species which have the highest absolute coefficients in each vector (i. e., considering the highest loadings by columns rather than by rows), determining their distributions, and from this information forming hypotheses about environmental factors which each vector might represent (Sprules 1977). Principal component 1 is most heavily loaded on Leptochelia, Malacoceros and Transennella, which occur predominantly at sites outside the sand dollar bed (except that they are scarce at station 8). This component represents the separation between Dendraster and tube builders. The species contributing most to principal component 2 are Anisogammarus, Cumella and Synchelidium shoemakeri, species which are most abundant in the summer samples and rare in the winter samples. Thus, principal component 2 represents seasonal variation. The third principal component overlaps somewhat with principal component 1. The species which contribute the most to it are Leptochelia, Eusyllis? and Lumbrineris zonata, with positive coefficients, and Paraphoxus tridentatus with a negative coefficient. P. tridentatus is abundant only at stations 1 and 8, where it

is one of the dominant species (Table 9). The other three species are rare at these locations. Thus, this component may represent an environmental difference between the more exposed stations at the mouth of the bay and other stations nearer its head.

Discriminant analysis completely separates the four groups (sand dollar bed in fall and winter, sand dollar bed in spring and summer, "outside" stations in fall and winter, "outside" stations in spring and summer), and the separation of each group from all others is statistically significant at the 1% level (Table 15). Two of the three canonical variables provided by the analysis account for 98.9% of the total dispersion. The 80 samples are plotted in relation to those variables in Figure 7. Clearly canonical variable 1 represents season, while canonical variable 2 represents the spatial separation between the sand dollar bed and the other sampling stations. The samples from station 8 fit into groups 3 and 4 and do not appear to be more appropriately classified with the sand dollar bed samples, nor do the high-density tanaid bed samples appear as outliers more appropriately placed in a separate group, as the cluster analysis had suggested.

The species which contribute significantly to the separation of the groups are listed in Table 16. Included in this list are the dominants P. spinosus, Cumella, Malacoceros and Eusyllis?, whose spatial and temporal distributions have already been detailed (Table 12). The

Table 15. F-matrix testing the separation of four site-season groups of the False Bay samples, based on discriminant analysis. Group 1=sand dollar bed in fall and winter. Group 2=sand dollar bed in spring and summer. Group 3=other stations in fall and winter. Group 4=other stations in spring and summer. Degrees of freedom=8,69.

	Group 1	Group 2	Group 3
Group 2	13.35		
Group 3	16.79	39.19	
Group 4	29.55	12.09	32.43

Table 16. A summary of the discriminant analysis of the False Bay data, giving the proportions of the total dispersion explained by the three canonical variables and the species and their coefficients used to calculate these variables.

	Canonical Variable		
	1	2	3
Cumulative Proportion of Total Dispersion	0.64500	0.98949	1.00000
Canonical Correlations	0.92718	0.87516	0.30123
Variable	Coefficients for Canonical Variables		
Paraphoxus spinosus	2.92739	1.87272	1.43174
Cumella vulgaris	-1.92976	-0.34678	0.32545
Malacoceros fulginosus	0.77186	-1.48508	0.44315
Eusyllis? sp.	0.66134	0.98331	-1.25212
Armandia brevis	3.31995	-0.12868	-1.10775
Paronella? sp.	4.51735	-5.22778	0.05539
Mysella tumida	0.88052	-2.44156	0.64907
Corophium insidiosum	3.99567	0.66416	3.14468
Lamprops sp.	1.94043	1.29697	4.04623
Constant	-7.48329	-2.16600	3.15031

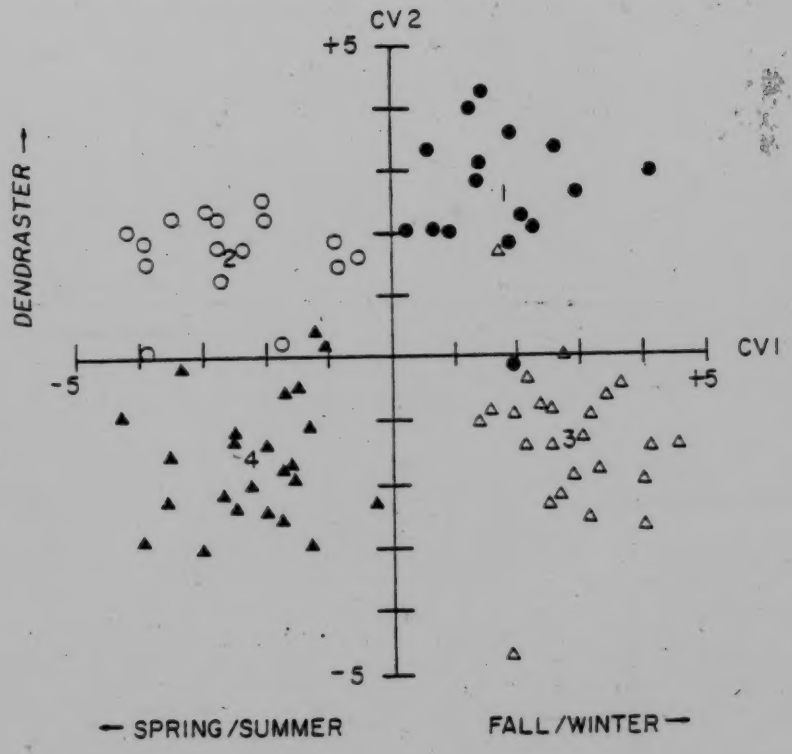
Figure 7. The 80 samples of False Bay infauna plotted in relation to canonical variables 1 and 2. Numbers indicate locations of the group means. The groups are identified as follows:

● 1- Sand dollar bed in fall and winter

○ 2- Sand dollar bed in spring and summer

△ 3- Other stations in fall and winter

▲ 4- Other stations in spring and summer


CV2
+5
DENDRASTER
CV1
-5
+5
-5
SPRING/SUMMER
FALL/WINTER
1
2
3
4

remaining species important to the separation are rare in most samples. Mysella tumida, a bivalve, is associated with the tube builders Leptochelia and Malacoceros (Table 14). Armandia brevis, a burrowing polychaete, shows a strongly seasonal abundance pattern, which has been described by Pamatmat (1966, 1968) and Woodin (1974), being absent from all but one of the summer samples. Although Armandia was significantly more numerous inside than outside the Dendraster beds surveyed in Chapter II, it did not show this distributional pattern in False Bay. Paronella?, an interstitial polychaete, is very rare in all samples, with a maximum density of 2.5 individuals/0.01m^2, but is most regularly encountered in the samples from stations 8 and 10. Corophium insidiosum, a tubicolous amphipod, and Lamprops sp., a burrowing cumacean, are also strongly seasonal, occurring primarily in fall and winter samples. Lamprops is associated with stations 1-4.

Although there was no a priori reason for including station 8 with the Dendraster bed stations, making the statistical test of the separation of the groups invalid (Green 1971), I did the analysis again including the samples from station 8 in groups 1 and 2. This modification also resulted in an apparently complete separation of the groups, with the station 8 samples fitting well into groups 1 and 2 and not seeming misclassified. The first two canonical variables accounted for 97.9% of the dispersion. The plot of the samples in relation to canonical variables 1 and 2

changed little from Figure 7, although the group centroids were shifted. The list of species contributing significantly to the separation was changed, with Eusyllis?, Paronella? and Mysella being replaced by Anisogammarus confervicolus and Axiothella rubrocincta. The latter is a tubicolous polychaete which was never encountered at stations 1, 2, 3, 4 and 8.

D. Discussion

Large temporal fluctuations in population densities apparently are common in benthic communities. Anderson (1972) found seasonal variations in the population densities of the dominant intertidal species in Morecambe Bay on the Irish Sea, while Moore (1978) noted seasonal shifts in the distributions of intertidal macrofauna in the Lower Mersey Estuary, U. K. Frankenberg and Leiper (1977) described order-of-magnitude density changes after six years and seasonal changes as great as three orders of magnitude in subtidal benthos. Green and Hobson (1970) reported a two-order-of-magnitude increase over one year in the density of a spionid polychaete.

Spatial structure characterized by the patchy distributions of dominant species also appears typical of soft sediment intertidal habitats. Anderson (1972) reported large variations in infaunal densities at a given shore level and felt the reasons for such variation were not

readily apparent. Green and Hobson (1970) measured significant differences in numbers of three abundant species among contiguous 6.0-m squares.

Both spatial and temporal factors, characterized by numerical fluctuations rather than by changes in species composition, have emerged as major forces in the structure of the False Bay infaunal community. Population densities of some species varied as much as three orders of magnitude among sampling stations and showed seasonal changes of two orders of magnitude, but the dominant species occurred at least occasionally at all sampling stations and in all seasons.

Population maxima of most of the dominant species not only fluctuated during the two years of this study but also differed from the observations of Pamatmat (1966, 1968). Although all of the eleven dominants were present during the earlier study, peak densities of P. spinosus, Leptochelia, Cumella and Anisogammarus recorded in the present survey were one to two orders of magnitude higher than those reported by Pamatmat. However, since sampling techniques and microhabitats sampled in the two studies differed, it is impossible to conclude that there has been any long term trend toward population increases.

It is perhaps surprising that the species composition of False Bay has remained so stable. Eagle (1973) reported faunal changes in the unstable mud of Liverpool Bay, characterized by loss of species washed out by turbulance

and their replacement by available larvae. On a smaller scale, Johnson (1970) noted changes in faunal composition in Tomales Bay, California, with replacement of some dominant species at 10 of 25 sites. I did not observe even this type of change, although the locations of greatest abundances of some species changed during the two years.

The spatial structure of False Bay is, in part, related to the presence of the Dendraster bed. The infauna of the bed (stations 1-4, Figure 5) is demonstrably different from that of the other sampling sites regardless of temporal fluctuations (Figures 6 and 7). It is characterized by relatively high densities of burrowing and epifaunal amphipods, particularly P. spinosus, Anisogammarus, Synchelidium and Pontogeneia and (with the exception of the tanaid bed at station 4, which appeared to abut on rather than occur in the sand dollar bed) reduced numbers of Transennella and of tube builders, particularly Malacoceros and Leptochelia (Table 12). The paucity of these organisms in the sand dollar bed was observed on the other Pacific Northwest beaches reported in Chapter II.

Environmental differences alone are inadequate to account for faunal differences between the Dendraster bed and the "outside" stations. Although organic content, sediment grain size and sorting coefficients are significantly different in the sand dollar bed than at the other stations, the differences are so small that they may not influence faunal distributions. Pamatmat (1966) felt

that differences in sediment grain size among the stations which he sampled were unimportant in determining the distributions of the False Bay infauna. In the present study, the coarsest sediments were found at station 8 and the finest at stations 2 and 3, but these locations have similar fauna (Figure 6).

The distributions of tube builders are also important to the spatial structure of the bay. Principal component analysis suggested a distinguishable assemblage composed of tube builders, their predators and small bivalves. This type of assemblage has been predicted by Woodin (1976), who theorized that small epifaunal bivalves which brood their young should reach their highest densities among tube builders. The most abundant bivalves in False Bay, Transennella tantilla and Mysella tumida, brood their young and occur in the upper 1-2cm of sediment (Pamatmat 1966; Chapter IV).

The principal component analysis can also be interpreted as suggesting that the tube builders in False Bay represent an environmental factor. Several authors (Fager 1964, Mills 1967, Rhoads and Young 1971, Young and Rhoads 1971) have provided evidence that tube builders do, in fact, modify the environment, stabilizing the sediment, increasing spatial complexity and altering median grain size. Thus, tube mats provide habitats for organisms which could not survive in the unmodified sediment.

Although both the sampling data presented here (Table

12) and in Chapter II and experimental evidence (Chapter IV) suggest that high densities of tube builders cannot coexist with sand dollars, Dendraster alone do not control the distribution of the False Bay tube mats. For example, locations of the highest density concentrations of Leptochelia changed during the two years of this study, but no alterations in the distribution of Dendraster were observed which could account for the change.

Shifts in locations of mats of Leptochelia may result from summer migration or mortality. Pamatmat (1968) observed large numbers of tanaids floating on the water during the summer. I have seen the same phenomenon and observed that tanaids held in the laboratory left their tubes and came to the sediment surface when the seawater inflow was inadvertently shut off. During summer low tides heat stress and/or anoxia must force Leptochelia to the sediment surface, where they are caught by the incoming tide and trapped by their hydrophobic carapaces in the surface film. Mortality of these individuals must be high, but perhaps a few survive to be carried to different locations where they may build new tubes. Regardless of their fate, such animals are removed from the original tanaid bed, contributing to a population decline at that site.

Reduced numbers of tube builders and increased densities of motile amphipods may also occur in the absence of Dendraster. Both cluster (Figure 6) and discriminant analyses suggest that station 8 has faunal affinities with

the sand dollar bed, including reduced numbers of Leptochelia and Malacoceros and high densities of Anisogammarus, Synchelidium (Table 12), and Paraphoxus tridentatus (Table 9).

Station 8, located nearest the mouth of the bay, is the most exposed of the ten stations. Its mean grain size is significantly higher than that of any other station (Table 5), suggesting that wave action is strongest there. Thus, the habitat at station 8 may undergo frequent disruption due to wave action, while similar disruption may occur in the sand dollar bed due to Dendraster's burrowing (Chapter IV). Although the reasons for instability differ, the net result at stations 1-4 and station 8 should be similar, creating an environment in which tube builders find it difficult to exist.

Elevated numbers of amphipods at station 8 suggest that the high numbers of amphipods in the Dendraster bed could be due to lack of tube builders rather than any positive association with sand dollars. Paraphoxus spp. are burrowers, which may be competitively inferior to tube builders as Woodin (1974) described for polychaetes.

Thus, it appears that both sand dollars and tube builders play major roles in the structure of the False Bay infaunal community. While the tube builders provide microhabitats for some organisms, the role of Dendraster in creating such habitats is less clear. However, the sand dollars are important because they limit the distribution of

tube mats and in this manner control the patchiness of microhabitats available to other infaunal species.

IV. An Experimental Evaluation of the Role of Sand Dollars in the Intertidal Community

A. Introduction

Experimental field studies have revealed that competition and bioturbation are much more important in the structuring of soft sediment communities than had previously been believed. Woodin (1974) demonstrated competition for space between tube-building and burrowing polychaetes, while Petersen (1977) showed interference (and suggested spatial competition) between the ghost shrimp Callianassa californiensis and the bivalve Sanguinolaria nuttallii. Orth (1977) found that disturbance of the sediment by cownose rays resulted in the loss of both individuals and species of infauna from a sea grass community. Wiltse (1977) noted that the presence of the moon snail Polinices duplicatus reduced the numbers of individuals and species not only of its molluscan prey but of polychaetes as well. She suggested that the loss of polychaetes resulted from the physical disturbance of the snails' burrowing. Virnstein (1977), studying predation on infauna by crabs and fish, was unable to eliminate disturbance of the sediment by the foraging activity of these predators as a cause of mortality. Woodin (1978) found that disruption of the sediment by horseshoe crabs (Limulus polyphemus) and blue crabs (Callinectes sapidus) resulted in reductions in both the number of species and abundance of infauna, but demonstrated that the

tubes of the polychaete Diopatra cuprea provided the smaller infauna with a refuge from this disturbance.

I have observed (Chapter II) that reduced numbers of tubicolous polychaetes and crustaceans occurred in areas dominated by sand dollars on ten beaches, and I have observed (Chapter III) that on one intertidal sand flat the faunal assemblage of a sand dollar bed is demonstrably different from the fauna not associated with sand dollars but is similar to that of a station characterized by wave disturbance, and that this difference has existed for at least two years.

The following experiments were designed to test for interactions between Dendraster and infaunal species and to elucidate the mechanisms of these interactions.

Disturbance of the sediment by sand dollars may adversely affect infaunal species which live at or above the depth to which sand dollars usually burrow. Species which, when disturbed, are slow to reburrow should be most severely affected. Both laboratory and field observations were used to determine the depth distributions and burrowing rates of selected infauna from False Bay. The depth to which sand dollars burrow and turn over the sediment was also measured in both the laboratory and the field.

To test whether observed infaunal distributions are actually due to negative interactions with Dendraster, sand dollar densities were manipulated by exclosure of animals from sand dollar beds or transfer to areas where Dendraster

had not previously been found.

B. Burrowing Behavior of False Bay Fauna

Methods and Materials

The burrowing behavior of sand dollars and of the smaller infauna was observed in both the laboratory and the field. These studies included depth distributions of the animals in the sediments, their burrowing rates and the rate of sediment turnover by sand dollars.

The depths to which sand dollars burrow in the field was observed on a low tide during mid-summer. A plastic ruler was pushed into the sediment until it contacted a sand dollar. The margin of the test reaching the greatest depth was identified, and the distance from this point to the sediment surface was recorded. When each measurement was completed, the animal was dug up to prevent its being remeasured.

The distance which sand dollars move during a 24-hour period was measured using the method of Ebert and Dexter (1975). At low tide a stake was placed in the sand dollar bed and all Dendraster within a 1.5-m radius of the stake were removed. One hundred animals were marked with nail polish and placed around the stake. On the following day's low tide all sand dollars within a 2-m radius of the stake were collected. The distances from the stake of all marked and unmarked animals were recorded at 0.5-m intervals. The

mean distance travelled in 24 hours was calculated from the frequency distribution.

Sand dollar movement was also measured by a second method. Four 1.0-m^2 plots in the sand dollar bed were marked with stakes. A 0.25m^2 quadrat subdivided into nine squares was placed successively in each quarter of each plot. Sand dollars were located by probing the sediment with fingers. Their positions were recorded on grids representing each 1.0m^2 plot with its 36 subdivisions. This procedure was repeated on four successive days. The minimum distance that the animals had moved each day was calculated as the minimum displacement of the sand dollars from their arrangement on the grid at day d required to produce their arrangement on day d+1. Animals which appeared in or disappeared from the quadrats from day to day were assumed to have done so by the most direct route. Mean displacements for each plot were calculated daily.

An experiment was designed to illustrate the effect of sand dollar burrowing on turnover of the sediments. A 0.09-m^2 plastic aquarium was filled to a depth of 8cm with sediments from False Bay. A 2-cm wide stripe of white sand (Sand'Art, Top Drawer, Inc., Newport, Oregon) was placed across the center of the aquarium at the sediment surface. Similar stripes of green, blue and yellow sand, respectively, were placed at 2-, 4- and 6-cm depths. Twelve sand dollars were added, and the aquarium was maintained for four days with constantly flowing sea water, except that the

water was drained to the sediment surface for two-hour periods at 24-hour intervals to simulate low tide.

The experiment was repeated using a $0.1m^2$ aquarium containing only five sand dollars. In this case, colored sand was obtained by spray-painting dried False Bay sediment with Fiesta Spray Enamel (Roxalin International, Toronto, Ontario). A cross of painted sand was placed at the sediment surface, and 0.5-cm deep layers of different-colored sands were layered with untreated sediment at 2-cm intervals to a depth of 10cm. The experiment was maintained in flowing sea water with daily "low tides" for one week.

Depth distributions of the other infauna in mid-summer were measured by taking sediment cores with a circular sampler (surface area: $40cm^2$) to a depth of 10cm. Each core was subdivided at 2-cm intervals. A total of 15 cores were taken, five each from stations 2 and 3 (Figure 5) and five between stations 6 and 7. Infauna were preserved and recovered as described in Chapter II. Data from all samples were pooled, and the percent of each species occurring at each depth interval was calculated. Due to taxonomic problems at the time of this experiment the spionid species and the two species of Paraphoxus were not separated.

The burrowing rates of common infaunal species were measured in the laboratory. Sediments were collected from False Bay and held in flowing sea water at 12-13C for no more than 3-4 days. As they were required for tests, animals were gently sieved from the sediments. Only intact,

apparently healthy animals were used. This requirement meant that several species of small crustaceans could not be tested, as it proved impossible to extract them undamaged. All animals were tested in flowing seawater at 12-13C. The larger animals (adult Leptosynapta, Transennella and the polychaetes) were tested in clear glass bowls filled to a depth of 8cm with the sediment from which the animals had been extracted. Smaller organisms (juvenile Leptosynapta and amphipods) were tested in 2-cm deep petri dishes filled with sediment. Sediments in the test vessels were changed daily. Timing began when the animal being tested was placed on the sediment surface and terminated as soon as the animal disappeared below the surface.

Results

In the field Dendraster burrowed to a maximum depth of 6.0cm. The mean depth at which sand dollars were found was 2.9±0.2cm. At other locations Dendraster may burrow more deeply. Chia (1969) reported sand dollars 10cm below the sediment surface at Alki Point, Seattle, Washington.

Ninety-four of the 100 marked sand dollars were recovered within 2m of the stake. Of these, 69 were within the 0.5-m radius, while only two had travelled more than 1.5m. The mean distance travelled by Dendraster in 24 hours was 42cm. Ten unmarked sand dollars were found within 1.5m of the stake, including four within the 0.5-m radius. Possibly some of these animals represented Dendraster which

had lost their marks.

The undisturbed sand dollars moved less than did those which had been placed near the stake. The overall average of the minimum distances that all of the observed animals were assumed to have moved was 14cm/day. The average distances calculated for each plot on each day are summarized in Table 14. While some of the Dendraster travelled at least 0.5m between low tides, one individual appeared not to have moved in 24 hours, and one did not move during the entire three-day study.

Since the former method overestimates the rate of sand dollar movement while the latter method underestimates it, the actual average rate of Dendraster movement must fall between 14 and 42cm/day.

Sediment turnover by sand dollars appeared similar in the two experiments. Within 12 hours of the beginning of the first experiment with 12 sand dollars, the white stripe had completely disappeared, and grains of white sand were distributed over the entire surface of the aquarium. Within 72 hours, green sand grains (from 2cm deep) appeared at the sediment surface and during the next day were distributed toward the ends of the aquarium. Colored sand from 4cm and 6cm never reached the surface, and these deeper stripes appeared undisturbed. Within twenty-four hours of the initiation of the second experiment with five sand dollars, colored sand from the surface cross was well distributed across the sediment surface. At 60 hours, colored sand from

Table 17. Means and standard errors of the minimum distances moved by False Bay sand dollars on three successive days. Values are given in centimeters. Sample sizes are recorded in parentheses.

	Day 1	Day 2	Day 3
Plot 1	13±4 (18)	13±3 (16)	12±2 (20)
Plot 2	16±4 (11)	24±5 (11)	15±4 (6)
Plot 3	12±3 (8)	10±3 (6)	22±6 (6)
Plot 4	13±2 (14)	13±3 (12)	11±2 (13)

the 2-cm level had reached the surface. By this time the sand dollars had aggregated in one corner of the aquarium, where they remained for the duration of the experiment. After 7 days, the 2-cm layer of colored sand had been obliterated in the area where the Dendraster were aggregated but remained visible in the rest of the aquarium. Colored sand from 4cm had been brought up to the 2-cm layer and surface sand had been carried down to 2cm in the immediate area of the sand dollars.

Although sand dollars apparently burrow somewhat more deeply in the field than in the laboratory, the observations described here suggest that Dendraster is capable of turning over at least the top two and probably the top 4cm of sediment.

The depth distributions of 11 infaunal species are compared with the mean and maximum depths of distribution of Dendraster in Figure 8. Only two of the polychaetes apparently dwell deep enough to avoid sand dollars.

Figure 9 shows the burrowing rates of the infauna tested. Male and female Leptochelia are represented separately, as their methods of burrowing are different. Females burrow rapidly, head first, and apparently build their tubes after they have disappeared below the sediment surface. Males move into the sediment tail first, picking up sand grains with their chelae and building tubes around themselves as they burrow.

The larger, deeper-dwelling species are generally the

Figure 8. Depth distributions (by percentage of the population) of benthic organisms from False Bay. Lines represent the mean and maximum depths at which sand dollars are buried on a summer low tide.

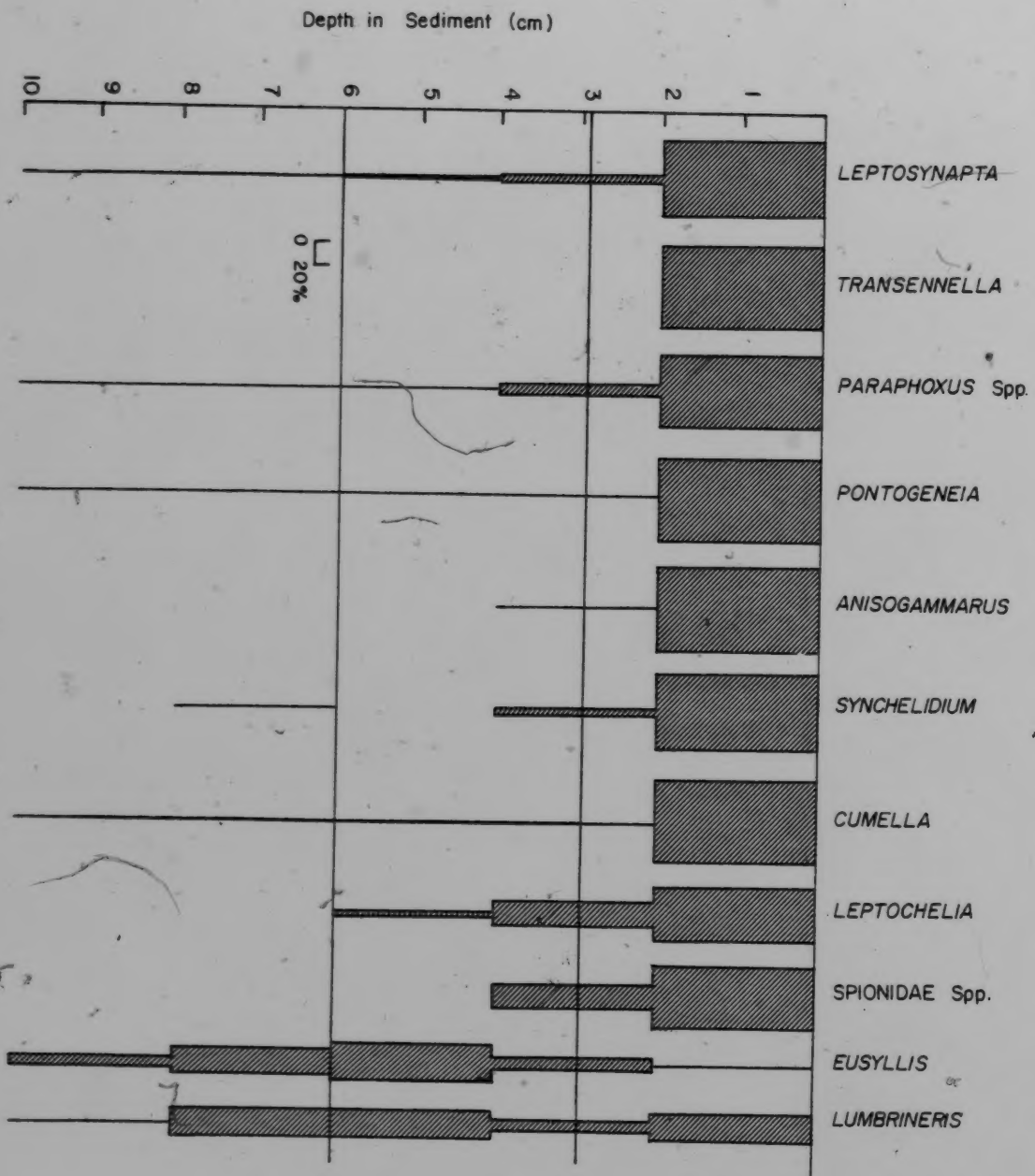
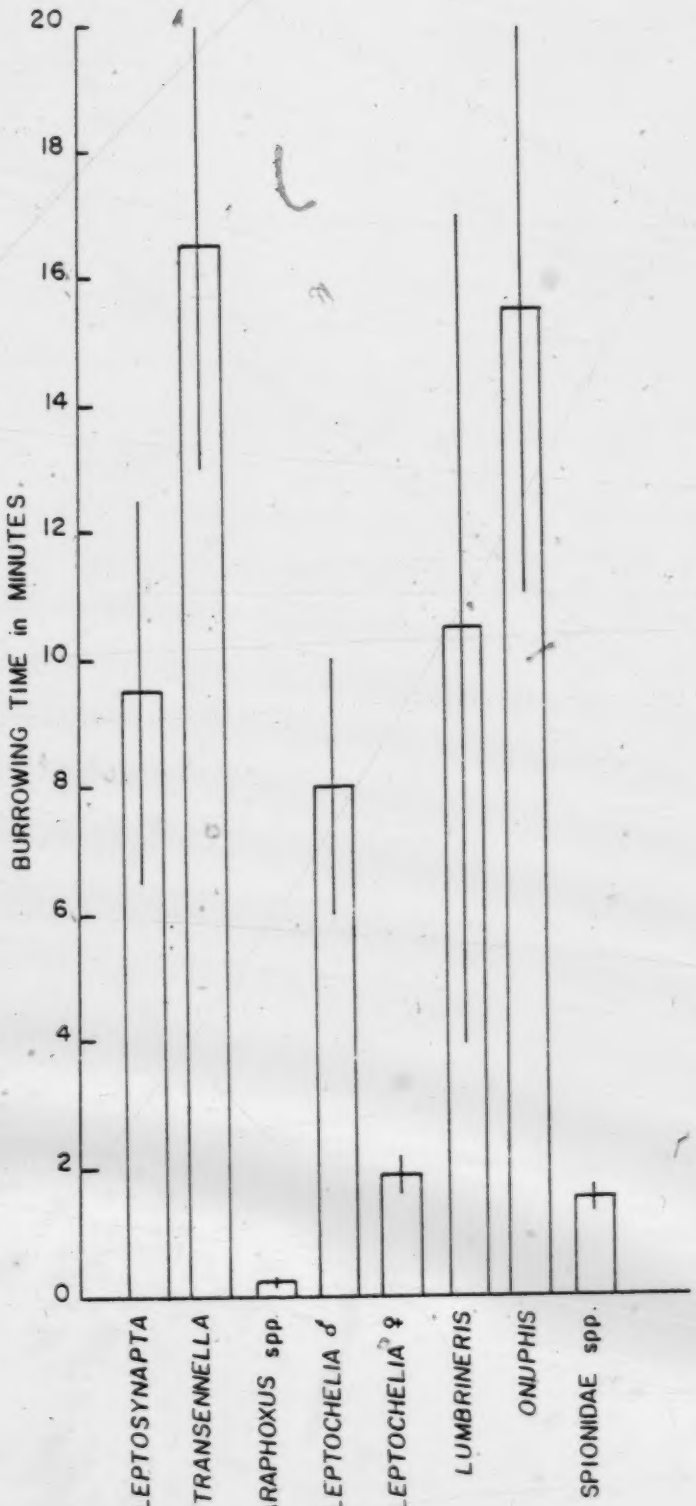

Depth in Sediment (cm)
10
9
8
7
6
5
4
3
2
1
0 20%
LEPTOSYNAPTA
TRANSENNELLA
PARAPHOXUS Spp.
PONTOGENEIA
ANISOGAMMARUS
SYNCHELIDIUM
CUMELLA
LEPTOCHELIA
SPIONIDAE Spp.
EUSYLLIS
LUMBRINERIS

Figure 9. Burrowing rates of benthic fauna. Values presented are means and 95% confidence limits of times required for animals to disappear below the sediment surface.


BURROWING TIME in MINUTES
0
2
4
6
8
10
12
14
16
18
20
LEPTOSYNAPTA
TRANSENNELLA
PARAPHOXUS spp
LEPTOCHELIA ♂
LEPTOCHELIA ♀
LUMBRINERIS
ONUPHIS
SPIONIDAE spp.

slowest burrowers. Transennella burrows rapidly once it extends its foot and begins to probe the sediment, but these clams apparently were disturbed by handling and remained closed for up to an hour after they were placed in the test vessels.

C. Faunal Manipulations

Methods and Materials

Densities and distributions of sand dollars were manipulated by confining or excluding the animals with cages. The same cage designs, sampling procedures and statistical treatments of the results were used through most of the experiments. Any variations from the general procedures outlined here will be noted when the experiments in which they occur are described.

Cages were constructed either of aluminum mesh with diamond-shaped pores, 2cm at their greatest dimension (1975-76 experiments), or of half-inch hardward cloth (preliminary and 1977 experiments). All cages were topless, 50cm on a side by 20cm high. They were sunk into the sediment to a depth of 10cm and secured with stakes at diagonally opposite corners.

Experiments were run for a maximum of 2 months, since it proved impossible to keep cages intact for longer than this period.

Infaunal samples, unless otherwise stated, were

collected to a depth of 10cm with a 0.01-m^2 corer. Samples were taken at least 8cm from the sides of cages to avoid edge effects. They were preserved and sorted as described in Chapter II.

Results of caging experiments were assessed using analysis of variance, followed, when warranted by significant treatment effects, by Student-Newman-Keuls multiple range tests (Snedecor and Cochran 1967). When Bartlett's tests revealed significant deviations from normality, the data were transformed using ln(x+1).

Preliminary Experiment, False Bay

In August, 1974, the infauna of the False Bay sand dollar bed (near station 2) and of a Dendraster-free area (near stations 6 and 7) were sampled with three circular cores, 40cm^2 X 10cm deep, taken randomly at each location. The samples were fixed in 10% formalin and stained with rose bengal and eosin Y for at least three hours before washing and sorting.

Two cages were erected in the Dendraster-free area. Sixteen adult sand dollars (the maximum density measured in the bed) were placed in one of the cages, while the second cage served as a control. After six days the infauna of the cages were sampled with three 40-cm^2 cores as previously described.

A list of the most common infaunal species encountered with their mean densities in the presence and absence of

Dendraster is illustrated in Table 8.

One-way analyses of variance followed by multiple range tests indicate that Leptosynapta, Transennella and spionid polychaetes are reduced in both the Dendraster bed and in the experimental cage as compared with the Dendraster-free area and the control cage.

False Bay Experiments, 1975-1976

In the spring and summer (April-August) of 1975 and 1976, I conducted a series of Dendraster-transfer and exclusion experiments. All experiments included cages with sand dollars (the test cages for transfer and controls for exclusion experiments), empty cages (the test cages for exclusion and controls for transfer experiments), and cage-free control plots. In most cases, the "sand dollar" cages contained three Dendraster each, the average number/0.25m^2, based on the population densities at stations 1, 2 and 3 (Table 7). A maximum of six Dendraster/cage was used in one experiment.

These experiments (whose results are summarized in Appendices 1-5) failed to reproduce the results of the preliminary study. Population densities of Transennella and the spionid polychaetes were not reduced in the presence of Dendraster. The effects of sand dollars on Leptosynapta were inconsistent. All experiments showed strong caging effects. Numbers of Leptosynapta, Transennella, Cumella and Anisogammarus were significantly reduced in cages compared

Table 18. Population densities of dominant infauna encountered in the preliminary experiment at False Bay. Values represent means and standard errors of three replicate $40cm^2$ X 10cm cores.

Species	Dendraster Bed	Dendraster-Free Area	Dendraster Cage	Control Cage
Leptosynapta	9.3± 4.4	36.7± 3.8	15.7± 5.2	33.0± 4.6
Transennella	0	12.0± 3.5	5.3± 1.9	12.3± 2.0
Paraphoxus spp.	150.0±17.9	365.7±39.9	263.7±14.9	240.0±34.8
Anisogammarus	38.3±12.7	35.0±13.6	11.0± 2.1	24.7± 4.8
Synchelidium	13.7± 4.4	1.7± 0.7	5.3± 1.4	3.3± 1.8
Cumella	52.7± 8.7	103.3±13.1	15.3± 4.8	8.3± 3.4
Leptochelia	0.7± 0.3	1.0	0	0.3± 0.3
Nebalia	0.7± 0.3	1.0± 0.6	0	0.3± 0.3
Eusyllis?	1.3± 0.7	14.3± 2.3	10.7± 2.2	9.7± 1.4
Lumbrineris	1.3± 0.3	1.0± 1.0	1.3± 0.3	0.3± 0.3
Spionidae spp.	0	5.0± 1.0	1.7± 0.3	4.7± 0.9
Onuphis	0.3± 0.3	4.0± 1.5	4.7± 2.4	1.0± 0.6
Nemertopsis	0	0	0	2.3± 1.4

with cage-free control plots, while Pontogeneia were more numerous in cages than in controls.

False Bay Experiments, 1977

The results of the 1975-1976 experiments suggested that sand dollars might have no significant effects at the low densities used, at least over the short term of these experiments. Alternatively, since Dendraster habitually aggregate the effects of low densities of the echinoids might be limited to a portion of a cage and appear only as high within-cage variance.

An experiment was therefore designed to test the effects of increasing densities of sand dollars on infaunal populations. Six densities of sand dollars (0, 6, 12, 24, 48 and 96 animals/0.25m^2) were caged in a tanaid bed near station 7 (Figure 5). The experiment was replicated in five blocks. Since it had proved impossible to eliminate caging effects, the impact of cages was held constant, and the population densities of infaunal species caged with Dendraster were compared with their densities in cages without Dendraster. The cages remained in place for two weeks in July; then four 100-cm^2 cores were taken from each cage, and the infauna were identified and enumerated.

Population densities of species among treatments were compared with analyses of variance and covariance, using the number of Dendraster as the covariate. The relation of increasing densities of Dendraster to the variance of

infaunal densities was tested with regression and correlation analyses.

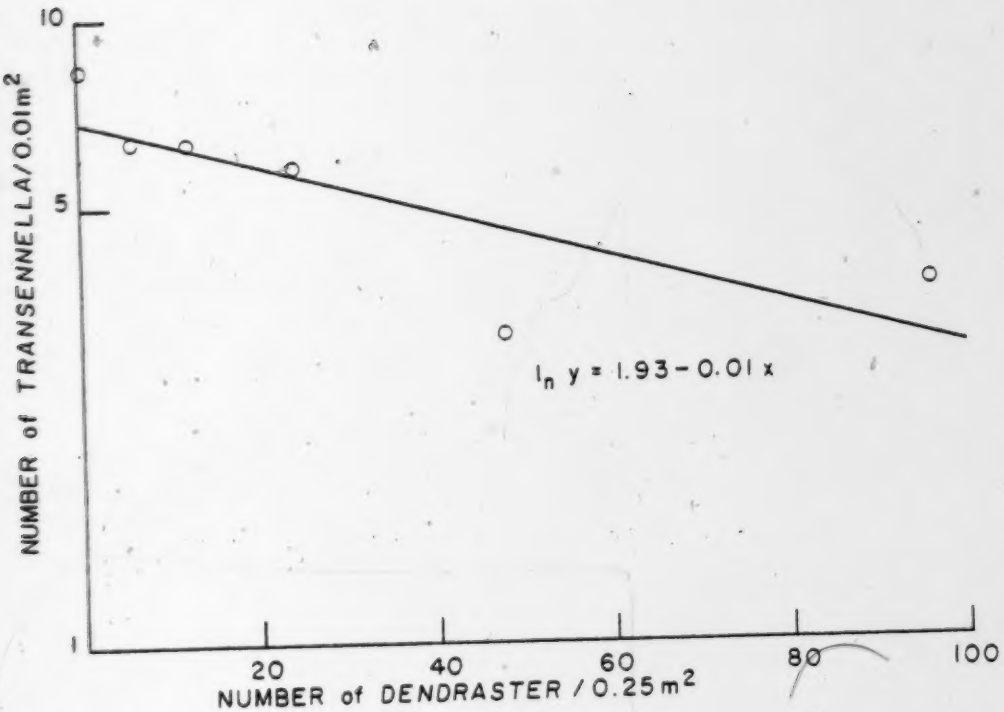
Most of the dominant False Bay infaunal species were affected by varying densities of Dendraster. Analysis of variance revealed significant effects on all species tested except the deep-burrowing polychaete Lumbrineris zonata (Table 19). Analysis of covariance produced significant regressions of Transennella, Paraphoxus, Leptochelia, spionids and all tube builders on sand dollar densities, (Figures 10, 11, 12), indicating direct responsiveness of these species to numbers of Dendraster. The density of Pontogeneia was significantly reduced only in the presence of 96 Dendraster, while the numbers of Synchelidium and Eusyllis peaked at intermediate densities of sand dollars. The responses of Leptosynapta and Cumella showed no interpretable patterns.

If at low densities sand dollars aggregated in one section of a cage and did not move enough to affect the whole area, their effect should have been patchy and should have increased the variance of the infaunal counts. Higher densities of sand dollars would have covered the entire cage area, producing a more even effect, and the variance should have decreased. Thus, the plot of variance against Dendraster density should have produced a unimodal curve with a maximum at relatively low densities. However, this pattern was not observed. The relation of the variance in tanaid counts to the density of sand dollars (Figure 13a) is

Table 19. Mean densities (number of animals/0.01-m^2 sample) of selected False Bay infauna after exposure to varying densities of Dendraster. The mean squared errors were obtained from analyses of variance in randomized blocks with ln-transformed data. (*P<0.05; **P<0.01) # indicates tube builders.

Species	Number of Dendraster/Cage 0	6	12	24	48	96	MSE	F(5,108)
Leptosynapta	6.8	4.4	6.6	5.1	4.3	5.5	1.32	2.70*
Transennella	8.3	6.5	6.2	5.7	3.1	3.7	1.44	7.58**
Paraphoxus spp.	142.6	127.1	132.2	141.2	83.7	58.3	1.28	10.59**
Pontogeneia	33.7	24.4	38.0	21.6	15.4	6.1	3.07	7.83**
Synchelidium	8.7	5.8	10.3	19.9	12.2	4.7	2.21	6.71**
Cumella	4.2	3.0	4.2	5.2	4.5	2.5	1.59	3.19*
Lumbrineris	8.8	7.8	7.4	7.0	8.1	7.5	1.39	0.38
Eusyllis?	6.6	8.3	12.4	8.8	6.1	6.8	1.71	2.33*
Leptochelia#	342.4	242.5	198.5	109.9	36.4	17.6	1.91	42.04**
Spionidae spp.#	85.8	38.0	68.6	62.1	26.2	5.8	2.13	25.85**
Total Tube Builders	447.2	311.7	280.6	182.2	69.5	24.7	1.67	46.87**

Figure 10. The relationship between the population densities of Transennella tantilla and Dendraster, based on the 1977 transfer experiment. Points plotted are means in five replicate cages.


10
5
1
NUMBER of TRANSENNELLA/0.01m²
ln y = 1.93 − 0.01 x
20
40
60
80
100
NUMBER of DENDRASTER / 0.25m²

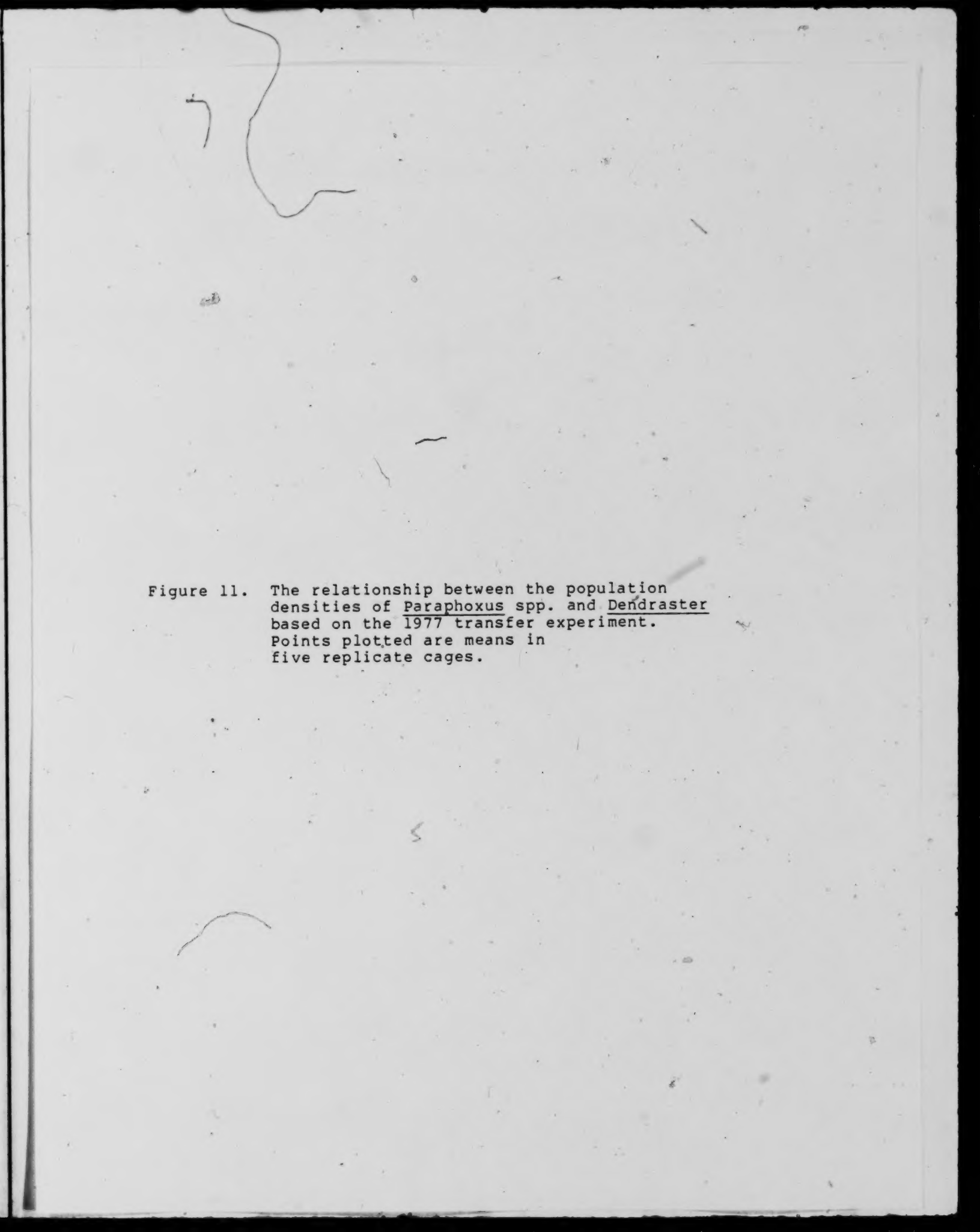


Figure 11. The relationship between the population densities of Paraphoxus spp. and Dendraster based on the 1977 transfer experiment. Points plotted are means in five replicate cages.

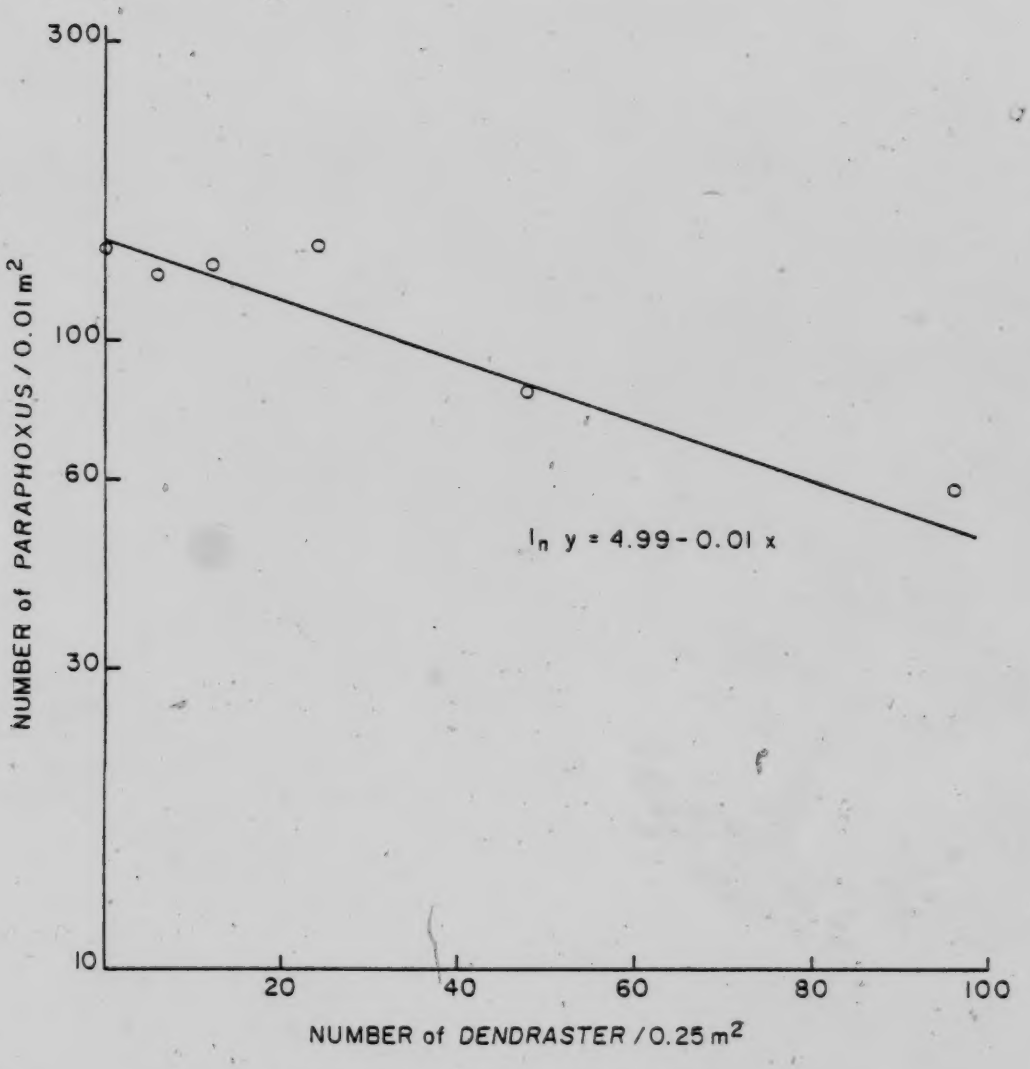

300
100
60
30
10
NUMBER of PARAPHOXUS / 0.01 m²
ln y = 4.99 - 0.01 x
20
40
60
80
100
NUMBER of DENDRASTER / 0.25 m²

Figure 12. The relationship between the population densities of tube-building species and Dendraster, based on the 1977 transfer experiment. Points plotted are means in five replicate cages.

○ All tube builders

● Leptochelia

△ Spionids

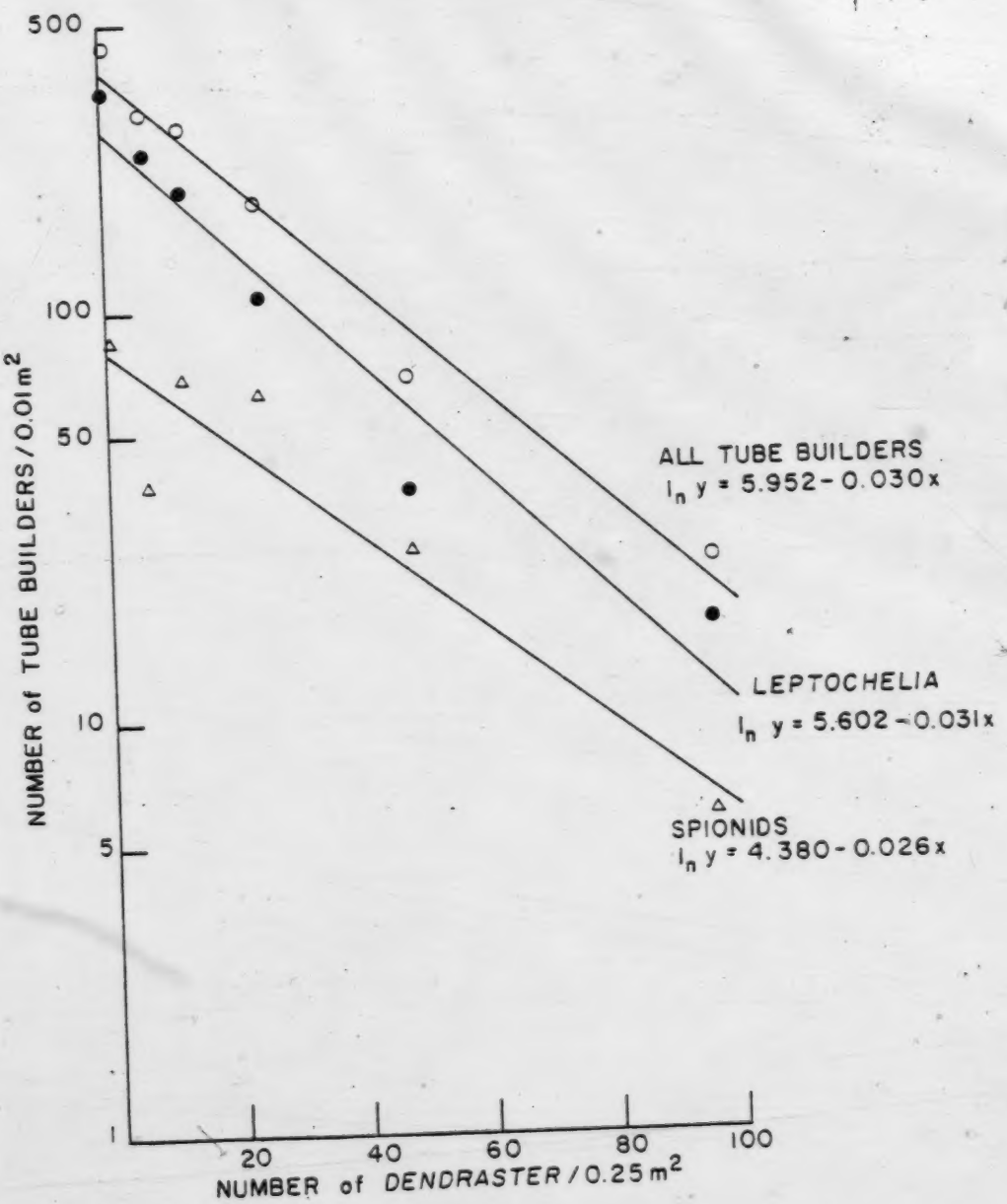
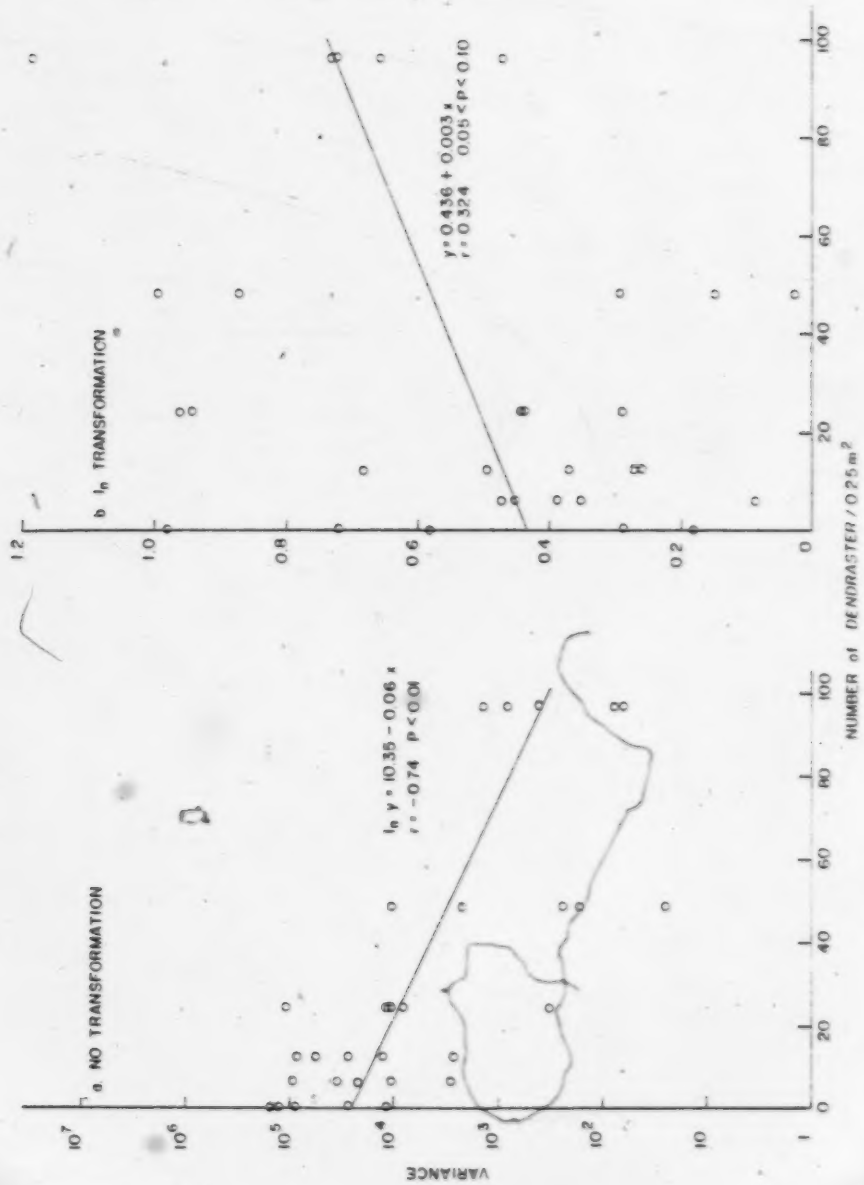

500
100
50
10
5
1
NUMBER of TUBE BUILDERS / 0.01 m²
ALL TUBE BUILDERS
ln y = 5.952 - 0.030x
LEPTOCHELIA
ln y = 5.602 - 0.031x
SPIONIDS
ln y = 4.380 - 0.026x
20
40
60
80
100
NUMBER of DENDRASTER / 0.25 m²

Figure 13. The relationship between the variance in the population densities of Leptochelia savignyi and Dendraster.


a NO TRANSFORMATION
$\ln y = 10.35 - 0.06x$
$r = -0.74$ $P < 0.01$
VARIANCE
b $\ln$ TRANSFORMATION
$y = 0.436 + 0.003x$
$r = 0.324$ $0.05 < P < 0.10$
NUMBER of DENDRASTER / 0.25 m²

typical of the pattern observed for most species. The curve shows no increasing phase; rather, the variance decreases steadily (and is significantly correlated with) increasing densities of sand dollars. Since the mean density of tanaids is decreasing at the same time (Figure 12), this relation is probably due to the correlation between mean and variance which is a statistical phenomenon of the contagious distribution of these animals. When the tanaid counts are log-transformed to remove the correlation between mean and variance, the correlation between variance and the density of sand dollars also disappears, but no unimodal curve is produced (Figure 13b). Even at low densities, Dendraster must be affecting the entire cage.

Partitioning the Effects of Dendraster

Sand dollars may reduce the densities of infauna either by occupying space and making access to the surface unavailable to other animals, or by disturbing the sediments and making it difficult for other species to maintain their positions. In an attempt to determine by which mechanism Dendraster exert their effect, I conducted the following experiment at False Bay.

Three blocks of four cages were placed in the tanaid bed near station 7, about 10m from the site of the previous experiment. The treatments included empty control cages, cages containing 48 live Dendraster, cages containing 48 cleaned Dendraster tests, and empty cages which were

disturbed by hand. The experiment remained in place for two weeks. Once a day during the first week, when the low tide exposed the cages, the "disturbed" cages were stirred by hand to a depth of approximately 10cm to simulate sand dollar burrowing. Since the tides of the second week were not low enough to expose the cages, the "disturbed" treatments were not stirred. On the fourteenth day, three samples were taken from each cage.

This experiment failed to separate a spatial effect from a disturbance effect of Dendraster on most species (Table 20). The densities of all tube builders, with species both pooled and considered separately, and of Cumella and Pontogeneia were lower in cages with live sand dollars than in any other treatment, but their numbers were not significantly different in either of the other cages than in the controls. Paraphoxus spinosus, Lumbrineris and Axiothella were not detectibly affected by any treatment. Synchelidium populations increased in both the "disturbed" and live sand dollar cages, but the "disturbed" treatment was not significantly different from either the sand dollar or the control treatments.

Some separation of the type of effect on Leptosynapta and Transennella was observed. These species were significantly reduced in the presence of both live sand dollars and cleaned tests, but not in the "disturbed" cages. For Transennella, but not for Leptosynapta, the "test" effect was significantly different from either the live sand

Table 20. Mean densities (number/0.01-m^2 sample) of False Bay infauna used to separate spatial effects from disturbance effects of Dendraster. The mean squared errors were obtained from analyses of variance in randomized blocks. The ANOVAS for Leptosynapta, Cumella and Leptochelia were based on ln-transformed data. (*P<0.05; **P<0.01)
# indicates tube builders.

Species	Empty Cage	Dead Tests	Hand Disturbed	Live Dendraster	MSE	F(3,30)
Leptosynapta	10.4	4.7	7.3	3.4	1.4	5.81**
Transennella	30.9	15.7	27.7	4.3	26.6	49.69**
Paraphoxus spinosus	251.1	175.6	214.2	192.1	3953.6	2.43
Pontogeneia	34.3	42.8	45.9	13.0	410.6	4.82**
Synchelidium	5.6	5.8	12.1	14.4	34.5	5.28**
Cumella	42.4	26.7	48.6	14.4	1.5	7.18**
Lumbrineris	14.9	11.2	13.7	9.7	36.4	1.37
Eusyllis?	14.4	10.2	9.8	4.7	43.4	3.32*
Leptochelia#	970.6	857.5	685.4	79.4	1.5	33.16**
Malacoceros#	45.1	46.4	74.4	13.1	769.1	7.36**
Axiothella#	2.6	2.9	2.8	3.0	8.0	0.04
Total Tube Builders	1066.7	943.3	792.4	150.0	57155.5	26.19**

dollar or the "disturbed" treatment. This result suggests that Dendraster occupies space which might otherwise be inhabited by Leptosynapta or Transennella. However, the addition of the tests itself may have created a disturbance for which there was no control. Therefore, the "test" effect could have been due to disturbance rather than occupation of space, although lack of effect in the "disturbed" cages suggests that this possibility is unlikely.

Effect of Dendraster on Sediments

The effect of Dendraster on the grain-size distribution of the sediment was studied in the following manner. Six cages were placed between stations 6 and 7. Three sand dollars were placed in each of two cages and six sand dollars each in two more cages. The remaining two cages served as controls. These cages were constructed of the aluminum mesh with diamond-shaped pores. After one month, one circular core ($40cm^2$ X 10cm) was taken from each cage and from each of two cage-free control plots. The cores were subdivided at 2-cm intervals. The sediments were dried and sieved.

Differences in sediment grain size among treatments were analyzed by split-plot analyses of variance and studentized range tests. The percentage of particles greater than 500μm diameter was used to calculate the statistic, as my preliminary observations suggested that the presence of these larger grains was the major difference between sand

dollar bed and sand dollar-free sediments. The percentages were transformed using the square root of (X+1/2) prior to analysis.

The addition of Dendraster produced a significant ($P<0.05$) effect on sediment grain size distribution. The percentage of particles greater than 500 µm varied significantly with both treatment (presence/absence of sand dollars) and depth. The depth X treatment interaction was also significant. In general, there was an increase in the percentage of coarser sand grains found at greater depths (Table 21).

The reason for this change in grain size distribution is unclear. Finer particles may have been transferred from deeper sediments by the sand dollars' burrowing activity and then lost from the sediment surface. However, since caging alone alters the sediment particle-size distribution in the same direction as the addition of sand dollars (although not significantly), the change in the sediments may also have been effected by alterations in current patterns caused by both cages and sand dollar tests.

Orcas Experiments, 1975-1977

The interactions between sand dollars and infauna were observed on two beaches in East Sound, Orcas Island (Figure 14). The infaunal community at Ship Bay was sampled in June, 1975, and faunal manipulations were conducted there in 1975 and 1976. In July, 1977, the Buck Bay community was sampled,

Table 21. Percentages of sediment particles >500μm diameter observed in the Dendraster-transfer experiment in False Bay, 1975.

Depth	No Cage	Empty Cage	Cage + 3 Dendraster	Cage + 6 Dendraster
2cm	4.25	4.45	3.30	4.00
4cm	3.75	4.20	3.75	3.80
6cm	4.50	3.70	5.10	4.15
8cm	4.25	4.40	5.75	6.70
10cm	3.45	5.00	6.65	7.05

Split-plot analysis of variance of sediment particle size distribution ($\sqrt{x+1/2}$ transformation). (*P<0.05; **P<0.01)

Treatment	df	SS	MS	F
Treatment	3	0.473	0.158	11.29*
Cage (Error #1)	4	0.056	0.014	--
Depth	4	0.793	0.198	6.60**
Depth X Treatment	12	1.070	0.089	2.97*
Error (#2)	16	0.480	0.030	--
Total	39	2.872	--	--

Figure 14. Map of East Sound, Orcas Island, Washington, showing the locations of the field experiments at Ship Bay (SB) and Buck Bay (BB).

SB
EAST SOUND
BB

and experiments were continued there that summer.

The Orcas Communities

The sand flat at Ship Bay is partitioned among three dominant macrofaunal species, sand dollars (400 predominantly adult animals/m^2), the tubicolous polychaete Mesochaetopterus taylori, and the bivalve Tresus capax. The three species appeared by visual inspection to form discrete patches, although some areas of overlap were observed.

The tide flat at Buck Bay is similarly partitioned between Dendraster (462 animals/m^2, about 50% of which are juveniles) and Mesochaetopterus. There are large patches of sand not occupied by either species, but Tresus is rare in these patches.

The infauna were sampled with five 0.01-m^2 cores taken from each type of patch at each of these sites. Since deep-dwelling fauna were present, these samples were taken to 15cm.

As noted in Chapter II, tube-building organisms appear consistently less frequently in samples from the sand dollar beds than in any other samples, but no species appears consistently over-represented among the Dendraster (Tables 22 and 23). However, several species, particularly Exogone, cirratulid polychaetes, and Pinnixa, appear associated with Mesochaetopterus. When an unfixed sample was gently washed in seawater to examine the living infauna, I observed that Exogone and the cirratulids attach their tubes directly to

Table 22. Mean densities and standard errors per $0.01m^2$ of dominant Ship Bay infauna. D=*Dendraster* bed, M=*Mesochaetopterus* bed, T=*Tresus* bed
# indicates tube builders.

Species	D	M	T
Mysella tumida	0.8±0.4	75.2± 8.7	4.6±1.7
Leptosynapta clarki	0	0	0
Cumella vulgaris	2.2±0.9	6.0± 3.6	8.2±3.4
Pinnixa sp.	0	12.8± 5.0	0
Leptochelia savignyi#	0.4±0.4	49.4±10.1	0.2±0.2
Corophium acherusicum#	0	7.6± 6.1	0.2±0.2
Ampelisca agassizi#	0	0	0
Exogone sp.#	0.6±0.2	218.0±25.8	2.6±1.4
Cirratulidae sp.#	0.6±0.4	30.6± 4.3	0.6±0.2
Spionidae spp.#	0.2±0.2	5.0± 1.0	0.4±0.2
Nereidae spp.#	0.6±0.2	2.8± 0.9	1.0±0.3
Owenia fusiformis#	0	0.4± 0.2	0.2±0.2
Nephthys caeca	0.2±0.2	0.6± 0.2	0.2±0.2
Scoloplos armiger	7.2±2.1	0.2± 0.2	0.4±0.4
Glycinde polygnatha	0	7.2± 1.4	0.2±0.2
Armandia brevis	0.2±0.2	0	2.4±0.9
Mediomastus capensis	0.6±0.2	29.0± 6.9	41.4±6.4

Table 23. Mean densities and standard errors per $0.01m^2$ of dominant Buck Bay infauna. D=*Dendraster* bed, M=*Mesochaetopterus* bed, O=other patches # indicates tube builders.

Species	D	M	O
Mysella tumida	87.0±55.1	123.6±29.8	3.8± 1.5
Leptosynapta clarki	0	3.0± 1.8	0
Cumella vulgaris	5.0± 0.6	10.4± 1.7	1.8± 1.0
Pinnixa sp.	0	2.8± 1.9	0
Leptochelia savignyi#	2.4± 1.0	3.4± 0.5	0.6± 0.2
Corophium acherusicum#	0	0.4± 0.2	2.2± 2.0
Ampelisca agassizi#	0	0.8± 0.4	33.6±27.1
Exogone sp.#	0.8± 0.4	121.4±49.9	1.8± 0.6
Cirratulidae sp.#	0	25.0±10.6	0
Spionidae spp.#	0	7.8± 3.1	14.6± 4.4
Nereidae spp.#	0	2.0± 0.5	0.2± 0.2
Owenia fusiformis#	0	2.8± 0.9	6.0± 2.1
Nephthys caeca	0.4± 0.2	1.0± 0.3	2.0± 0.7
Scoloplos armiger	2.8± 1.1	0	2.8± 2.1
Glycinde polygnatha	0.8± 0.4	1.6± 0.4	3.4± 1.6
Armandia brevis	17.8± 5.8	4.8± 3.2	0.4± 0.2
Mediomastus capensis	0.4±0.2	2.8± 0.5	1.8± 0.7

the Mesochaetopterus tubes.

Faunal Manipulations

In July, 1975, a transfer experiment was conducted at Ship Bay, using the aluminum cages with diamond-shaped pores. Eight cages were placed on a section of the sand flat occupied by Mesochaetopterus. Four cages were placed in the sand dollar bed. The presence of numerous shell fragments made it impossible to sink these cages more than 5cm into the sediment. The number of Mesochaetopterus tubes in each cage was recorded. All sand dollars were removed from the cages; then 40 adults were returned to each of the cages in the Dendraster bed, and 40 adults each were placed in four of the cages in the polychaete bed. Two weeks later, eight similar cages were placed in the clam bed. The number of Tresus siphons observed in each cage was recorded, and 40 adult sand dollars were added to each of four of the cages. After four weeks (six weeks after the beginning of the polychaete experiment), the sand dollars were removed from each cage and counted. The numbers of Mesochaetopterus tubes and Tresus siphons in each cage were recorded. The changes in numbers of polychaetes or bivalves with and without sand dollars were compared by Student's t-tests.

The number of Mesochaetopterus was significantly ($P<0.05$) reduced in the presence of Dendraster. Tubes disappeared from three of the four cages containing sand dollars, while the number of tubes increased in all cages

without sand dollars. Apparently Dendraster both prevents settlement of recruits and adversely affects established polychaetes. However, rather than indicating reduced numbers of Mesochaetopterus, the observed difference could have been due to reduced visibility of tubes, if Dendraster only caused the loss of the portions of the tubes which normally protrude above the sediment surface.

None of the other comparisons yielded significant results, but fewer than the original 40 sand dollars remained in all cages containing Mesochaetopterus and Tresus (losses ranged from one to 12 animals/cage, except that 20 disappeared from one cage in the Mesochaetopterus bed which pulled loose, allowing the sand dollars to escape), while animals were lost from only one cage in the sand dollar bed. Empty tests showing evidence of predation by birds were observed in cages containing clams. Sand dollars did not appear buried as deeply in the presence of bivalves and polychaetes as they were alone. Thus, there is a suggestion that sand dollars may be excluded by polychaetes and bivalves.

In June, 1976, an exclusion experiment was conducted at Ship Bay. Eight cages were placed in the sand dollar bed. All sand dollars were removed and counted. Eighty adults (the mean number per $0.25m^2$) were returned to each of four cages. Sand dollars were excluded from the remaining cages. After eight weeks, one sample ($0.02m^2$ X 15cm) was taken from each cage and from each of four randomly-selected uncaged

sites in the sand dollar bed. Samples were preserved and sorted as previously described, except that the animals were stained with rose bengal to facilitate sorting. Differences in population densities of infaunal organisms were compared by one-way analyses of variance.

Two species, the tubicolous polychaete Owenia fusiformis and a gastropod Alvinia sp., which had not previously been encountered in the Ship Bay sand dollar bed, appeared following the removal of Dendraster (Table 24). Alvinia remained so rare that the difference between the exclusion and the remaining cages was not statistically significant, but the difference for Owenia was significant at the 5% level. No other individual species was significantly increased by the removal of sand dollars, but densities of the polychaetes Armandia brevis and Magelona sp. were significantly lower in all cages than in the uncaged controls. Most tubicolous species which had been observed in the Mesochaetopterus bed appeared so infrequently that their numbers were not analyzed statistically; however, the pooled counts of all tube builders (crustaceans, polychaetes and phoronids) were significantly higher in the Dendraster-removal cages than in either of the other treatments ($P<0.01$). Pooled counts of all motile crustaceans (amphipods, cumaceans, and crabs) were significantly higher in the cages containing sand dollars than in the empty cages or cage-free plots ($P<0.05$).

In August, 1977, I conducted a sand dollar removal

Table 24. Treatment means (number/0.02-m^2 sample) from the Dendraster-exclusion experiment at Ship Bay, Orcas Island. The mean squared errors were based on one-way analyses of variance. The ANOVA of total tube builders was based on ln-transformed data. (*P<0.05; **P<0.01)
# indicates tube builders.

Species	No Cage	Dendraster Cage	Empty Cage	MSE	F(2,9)
Mediomastus capensis	5.2	5.2	17.0	127.7	1.44
Armandia brevis	29.8	5.5	8.0	138.4	9.01**
Magelona sp.#	7.0	0.8	2.5	28.4	1.46
Owenia fusiformis#	0.0	0.0	8.0	12.7	6.74*
Alvinia sp.	0.0	0.0	3.0	3.8	3.18
Total Bivalves	7.0	15.0	69.8	4375.4	1.07
Total Motile Crustaceans	2.0	5.2	2.2	2.4	5.48*
Total Tube Builders	11.6	3.3	14.4	1.3	9.72**

experiment at Buck Bay. Since currents at this site caused rapid destruction of the standard cages, the caging design of this experiment had to be altered. Only one 1m X 2m cage was used. It was constructed of 1/2" hardware cloth pressed 10cm into the sediment and was supported on all sides with rocks. After eight weeks, 16 samples (10 X 10 X 10cm) were taken from this cage and from an adjacent 1m X 2m control plot. I assumed that the effects of the cage would be in the same direction, but not necessarily the same magnitude, as those produced by the cages of the previous studies. However, since there was no control for caging effect, the results of this experiment must be considered tentative.

Differences in infaunal densities between the removal cage and control plot were compared using t-tests. The tubicolous amphipod Ampelisca agassizi, and the polychaetes, Owenia, Nephthys caeca and Glycinde polygnatha were all significantly ($P<0.05$) more numerous in the sand dollar removal cage than in the control plot (Table 25). The density of Armandia brevis was lower in the removal than in the control plot, but based on the results of the experiment at Ship Bay, this difference may be a caging effect rather than a positive association between Armandia and Dendraster. Neither the pooled total of tube builders nor of motile crustaceans was significantly different in the two treatments.

The variance in the total number of tube builders was extremely high because some of the control samples contained

Table 25. Treatment means and standard errors from the *Dendraster*-exculsion experiment at Buck Bay, Orcas Island. Values represent numbers of animals/0.01m^2 sample. (*P<0.05, **P<0.01) # indicates tube builders.

Species	Exclusion	Control	t
Ampelisca agassizi#	0.8±0.3	0.1± 0.1	2.64*
Owenia fusiformis#	1.7±0.2	0.2± 0.1	5.49**
Platynereis bicanaliculata#	1.8±0.5	19.1±10.8	1.60
Mediomastus capensis	2.7±0.6	2.1± 0.6	0.82
Nephthys caeca	3.9±0.6	1.0± 0.3	4.07**
Scoloplos armiger	1.2±0.3	1.8± 0.4	1.04
Glycinde polygnatha	2.9±0.4	1.4± 0.4	2.41
Armandia brevis	1.1±0.3	17.9± 3.5	4.82**
Total Tube Builders	11.1±2.0	31.7±14.8	1.38
Tube Builders except *Platynereis*	9.2±1.6	12.6± 5.1	0.62
Total Motile Crustaceans	6.9±0.9	8.3± 1.1	1.05
Total Bivalves	8.5±3.2	38.1±22.8	1.28

large sheets of ulvoid algae to which were attached the tubes of Platynereis bicaniliculata. Ten or more worms might be attached to a single sheet (about 100cm^2) of algae, and there were as many as 142 Platynereis per sample. Spionid polychaetes and the amphipods Corophium acherusicum and Photis brevipes were also present on the algae, and in some cases their tubes appeared attached directly to the nereid tubes. Not all samples which contained algae had high densities of Platynereis, but the tube builders were absent from samples which lacked algae. These organisms, then, do not represent part of the sand dollar bed fauna but must be considered accidentals which were carried there with the drift algae.

D. Discussion

The depth at which an organism lives determines its susceptibility to surface disturbance agents. Species which live near the sediment surface are most susceptible to predation by crabs and fish, while those which dwell deep in the sediment or which can retract quickly are least affected (Virnstein 1977). Animals whose tubes lie at depths of sediment disturbed by blue crabs and horseshoe crabs succumb, while those whose tubes penetrate more deeply escape this source of mortality (Woodin 1978).

I have demonstrated that sand dollars disturb the sediments. In the laboratory, their burrowing can turn over

at least the upper 4cm of sand, but in the field they affect the grain size distribution of the sediment to a depth of 10cm (Table 21). This action should affect animals living in at least the upper few centimeters of sediment.

The behavior of an organism should influence the way it responds to sand dollars. A species which is slow to reburrow should suffer more severely if overturned than would a rapid burrower. Tube builders, which must repair damaged tubes, should suffer from disturbance even though they might reburrow quickly. On the other hand, motile crustaceans, particularly epifaunal species, might not only resist disturbance by Dendraster but might respond positively to sand dollars by taking refuge among them.

Most of the species commonly encountered at False Bay reside primarily or exclusively in the upper 3cm of sediment (Figure 8). Leptosynapta, Transennella and Leptochelia (particularly the males) are also relatively slow to reburrow (Figure 9). These species, with the spionids which must rebuild their tubes after burrowing, should suffer most severely from bioturbation.

As predicted, the densities of Transennella, Leptochelia and the spionids, as well as the combined totals of all tubicolous species, declined with the addition of increasing densities of sand dollars (Table 19). The deeper burrowing Lumbrineris and Eusyllis? did not respond negatively to Dendraster.

Removal of Dendraster from the two Orcas Island sites

reaffirmed their negative effect on tube builders (Tables 24 and 25). The total numbers of all tube builders and the numbers of Owenia in particular increased at Ship Bay, while the densities of Ampelisca and Owenia increased at Buck Bay after exclusion of sand dollars.

Owenia appears particularly ill-suited to coexisting with Dendraster. I was unable to induce any of these polychaetes to abandon their tubes. They attempted to reburrow while still in the tubes but remained half-exposed at the sediment surface after 12 hours. Although the adults of this species may be large enough to penetrate the sediment below the influence of Dendraster, juveniles which must live nearer the sediment surface should not be able to establish themselves in sand dollar beds. Indeed, Owenia did not occur in either Orcas Island sand dollar bed (Tables 22 and 23), and with the exception of one individual at Buck Bay, all the Owenia which appeared following the removals of Dendraster at both sites were juveniles.

In general, the responses of individual species to the addition or removal of Dendraster were consistnet with their observed distributions in the Pacific Northwest (Chapter II), as well as in False Bay (Chapter III). Transennella, Leptochelia, Malacoceros, Ampelisca and Glycinde, which were less numerous inside than outside the sand dollar beds, responded negatively to Dendraster (Tables 19, 20, 25). Cumella and Leptosynapta, whose distributions in False Bay apparently were affected less by sand dollars than by other,

undescribed factors (Table 11), responded inconsistently to the addition of Dendraster (Tables 19 and 20).

Increases in populations of species following the removal of Dendraster were no doubt determined not only by the organisms' initial incompatability with sand dollars but also by the availability of recruits. Opportunistic species, with high recruitment rates and many reproductions a year, are usually the first to colonize any newly-opened patch. Owenia fusiformis and Ampelisca abdita are among the opportunists which McCall (1977) lists as settling in defaunated mud placed in Long Island Sound. O. fusiformis and a different species of Ampelisca, A. agassizi, appeared following the removal of sand dollars at Orcas.

The response of motile crustaceans to Dendraster was not consistent. At False Bay Synchelidium increased at intermediate densities of sand dollars (Table 19). At Ship Bay the total number of motile crustaceans, including crabs, amphipods and cumaceans was higher in cages containing sand dollars than in empty cages (Table 24). However, the latter result was not repeated at Buck Bay (Table 25), and populations of two False Bay amphipods, Paraphoxus and Pontogeneia, decreased at high densities of Dendraster (Table 19). Since numbers of Synchelidium also increased in hand-disturbed cages (Table 20), this species may have been responding to changes in sediment stability or to the removal of a competitor rather than responding directly to sand dollars.

Types of Interactions of Sand Dollars with Infauna

Sand dollars differ from other organisms which disturb the sediments in an important way. The rays, moon snails, fish, blue crabs and horseshoe crabs whose effects have been reported (Orth 1977, Wiltse 1977, Virnstein 1977, Woodin 1978) are all epifauna which pass through an area causing transitory disruption. Although sand dollars are capable of travelling at least 0.5m in 24 hours, left undisturbed they may move only a few centimeters in several days, and a sand dollar bed may persist on the same portion of a beach for years. Thus, Dendraster more-or-less permanently occupy space in the sediment and may compete with the infauna rather than simply disrupting them.

The occupation of space by sand dollars may have important consequences for at least some of the infauna. Numbers of Leptosynapta and Transennella were significantly reduced by the addition of empty tests as well as by live Dendraster (Table 20). Transennella and newly-recruited Leptosynapta are confined to the upper 2cm of sediment where they may be out-competed for position by a dense population of sand dollars. Although tube builders failed to respond significantly to the empty tests, they may not be able to compete successfully for space with Dendraster. Leptochelia built their tubes on top of the empty tests, but they could not build tubes on live sand dollars.

In one of the experiments at Ship Bay, Mesochaetopterus densities apparently decreased following the addition of

sand dollars. Since the tubes of these polychaetes penetrate too deeply into the sediments to be overturned by Dendraster, the sand dollars must have affected the worms in some other manner, perhaps by overlying the openings of their tubes and denying them access to the sediment surface.

Hand disturbance did not significantly reduce infaunal populations, although the numbers of most species in the hand-stirred cages were lower than in the control cages. Virnstein (1977) similarly noted that hand disturbance had little effect on most infauna and suggested that foraging by crabs might cause more severe disruption than he was able to simulate. Because my hand-stirring was a transitory rather than a continuous disturbance, it may have been less severe than burrowing by sand dollars. Further, the populations in the disturbed cages had a week to recover before they were sampled. Species adapted to life on a sand beach, where the sediment is regularly disturbed by wave action, should be able to recover quickly from mild transitory disturbances.

The results of the hand-disturbed and empty-test treatments were intermediate between the effects of live sand dollars and control cages, and only the live Dendraster had a statistically significant effect on the densities of most species. These results suggest that sand dollars affect the infauna both by disrupting the sediments and by occupying space.

It is also possible that sand dollars may exclude some species by a method not investigated here, perhaps by

consuming larvae or juveniles. Timko (1975) found that Dendraster will accept a wide range of food items, including brine shrimp and their own (Dendraster) larvae, but she did not report either larvae or juveniles of benthic invertebrates as components of sand dollar gut contents. Chia (1969) included "limbs of small crustaceans" among Dendraster's gut contents, but did not report the proportion they comprised. I looked at the gut contents of six Dendraster each from False Bay and Buck Bay and could not find either larvae or, apart from one nematode, fragments of benthic invertebrates.

Thus, Dendraster should be considered a superior competitor for space in the intertidal, rather than a predator or a transitory disturbance agent similar to Wiltse's (1977) Polinices or Woodin's (1978) Limulus and Callinectes.

V. General Discussion

A rigorous definition of a community is impossible to provide (Mills 1969). Rather, marine ecologists are beginning to view the community as a spatial and temporal mosaic (Johnson 1970, Levin and Paine 1974) in which part of the community undergoes perturbation without any immediate effect on the surrounding areas . Thus, patches are formed, creating environmental heterogeneity and interrupting natural successional sequences. In such communities opportunistic species, which would be excluded by a dominant spatial competitor, are able to persist.

Some authors have attempted to model this type of community. Levin and Paine (1974) have predicted rates of patch formation and closure. Woodin and Yorke (1975) have emphasized the persistence of species, describing a system in which different organisms occupy large patches, from which neither can evict the other in the absence of disturbance, but one species can invade and grow if introduced to an unoccupied patch. This type of community cannot persist without perturbation.

The False Bay and Orcas Island communities, as well as the sandy beaches in Washington and British Columbia which I have investigated, are characterized by patchiness. Sand dollar beds, of course, are patches. Tube builders are also patchily distributed, and there are areas of sand not occupied by either Dendraster or tube mats.

Both the observational and experimental evidence presented here indicate that tube builders and their associated fauna occur in reduced numbers in sand dollar beds. The tubicolous crustaceans Corophium spp., Ampelisca agassizi and Leptochelia savignyi, the spionid polychaete Malacoceros arenicola, and the bivalve Transennella tantilla, as well as the total number of tube builders, were all significantly ($P<0.05$) less numerous inside than outside the sand dollar beds on the ten beaches sampled (Chapter II). Similarly, Leptochelia, Malacoceros fulginosus and Transennella were consistently less abundant inside the Dendraster bed than at the "outside" stations during the two-year False Bay study (Chapter III). Numbers of Transennella, Malacoceros and Leptochelia, as well as the pooled totals of all tube builders, decreased significantly with increasing densities of Dendraster at False Bay, while Ampelisca, the tubicolous polychaete Owenia fusiformis and the total numbers of tube builders increased significantly following the removal of sand dollars at the two Orcas Island sites (Chapter IV).

There is also some suggestion that sand dollars have difficulty invading tube mats. The mortality rate of Dendraster transferred to patches of Mesochaetopterus tubes was higher than in the sand dollar bed, and the Dendraster appeared to have difficulty burrowing among the tubes. This impression is supported by the experiments of Backman (1977), who found that Dendraster could not burrow in the

rhizome mat of Zostera marina but could invade areas from which the eelgrass had been removed. Sand dollars may also be limited by smaller tube builders. Highsmith (1977) observed that the survival of newly-metamorphosed Dendraster was significantly reduced by the presence of Leptochelia. Although adult sand dollars are capable of eliminating Leptochelia, apparently recruitment of Dendraster into tanaid beds is unlikely. Thus, a dynamic equilibrium of the type described by Woodin and Yorke (1975) may exist between sand dollars and tube builders.

The presence of tube mats appears to be a major structuring force on the beaches described in this study. Many authors (Fager 1964, Mills 1967, Rhoads and Young 1971, Young and Rhoads 1971, Woodin 1976) have discussed the importance of tube builders in providing habitats for other organisms, and this function was observed here. Mesochaetopterus provides a substrate for other tube builders and a habitat for small bivalves. The Leptochelia-Malacoceros association in False Bay also is a habitat for small clams. The Mesochaetopterus beds may function more broadly as a refuge from Dendraster or other sources of disturbance as does Diopatra cuprea (Woodin 1978). Several species of small tube builders which were not abundant elsewhere were observed among, but not attached to, the Mesochaetopterus tubes. Conversely, abundance of tubicolous polychaetes reduces numbers of burrowing worms (Woodin 1974). Burrowing amphipods are less numerous in the

tube mats in False Bay than elsewhere.

Since tube mats provide habitats for some species while limiting the distributions of others, the causes of their patchy distributions are of major importance to the overall structure of the sand beach community. Disturbance by burrowing organisms including snails and crabs (Wiltse 1977, Woodin 1978) and washing-out due to turbulance during storms (Mills 1967, Eagle 1973) can create patches in tube mats. However, tube builders can resist or recover quickly from some types of physical disturbance. McGrorty et al. (1976) found that although the visible effects of hovercraft on the sand in their flight path were marked, no species, including spionid polychaetes, was significantly more or less abundant in the flight path than in adjacent areas. Similarly, Leptochelia and Malacoceros were not affected by my hand disturbance.

Sand dollar beds are less important than tube mats as structuring forces in that they do not consistently provide habitats for other organisms, and there is nothing which can be recognized as a "sand dollar bed community." However, the burrowing polychaete Armandia brevis is significantly more numerous in sand dollar beds (Table 2), and numbers of this species apparently decreased following the removal of Dendraster at Buck Bay (Table 25). In some instances (False Bay and the experiment at Ship Bay, Orcas) motile crustaceans appear more numerous in association with Dendraster than elsewhere, although in False Bay the

burrowing amphipods are also more numerous in a site characterized by wave disturbance, where tube builders occur in reduced numbers. Since Woodin (1974) has shown that the numbers of Armandia increase following the removal of tube builders, the abundance of both this polychaete and the False Bay amphipods may be due to the lack of competing tube builders rather than to any positive response to sand dollars.

The major role of Dendraster in the intertidal sand flat community appears to be that of a dominant competitor, which occupies space and disturbs the sediment sufficiently to prevent the establishment of tube mats and their associated fauna.

Transfer experiments (Tables 18 and 19) suggest that sand dollars are also capable of functioning as disturbance agents to open patches in mats of small tube builders. Such disturbance should occur if sand dollar beds shifted seasonally, as Morin (personal communication) observed in subtidal beds, or when a few sand dollars moved to areas outside a bed, as I observed in False Bay, or when individual Dendraster were washed out of the bed by waves and then returned, as their trails on the sediment surface at several sites indicated. However, the effect of a few Dendraster's moving and remaining in a new area only briefly might be negligible, as at least Leptochelia and Malacoceros are able to recover quickly from mild, transitory disturbances.

The intertidal sand flats studied can be characterized as the temporal mosaics described by Johnson (1970), Levin and Paine (1974) and Woodin and Yorke (1975). Mats of tube builders with their associates are patchily distributed in time and space. Sand dollars are important in this system in that they contribute to the patchiness by their behavior of congregating in beds and to the extent that they limit the distribution of, or open patches in, mats of tubicolous species.

References

Anderson, S. S. 1972. Ecology of Morcambe Bay. 2. Intertidal invertebrates and factors affecting their distribution. J. Appl. Ecol. 9: 161-178.

Armstrong, J. W., C. P. Staude, R. M. Thom and K. K. Chew. 1976. Habitats and relative abundances of the intertidal macrofauna at five Puget Sound beaches in the Seattle area. Syesis 9: 277-290.

Backman, T. W. 1977. Displacement of eelgrass, Zostera marina, by the sand dollar, Dendraster excentricus, at Puget Sound. Paper presented at the Western Society of Naturalists 58th Annual Meeting, Dec. 27-30, 1977.

Bell, S. S., and B. C. Coull. 1978. Field evidence that shrimp predation regulates meiofauna. Oecologia 35: 141-148.

Bernstein, B. B., R. R. Hessler, R. Smith and P. A. Jumars. 1978. Spatial dispersion of benthic Foraminifera in the abyssal central North Pacific. Limnol. Oceanogr. 23: 401-416.

Birkeland, C., and F. S. Chia. 1971. Recruitment risk, growth, age and predation in two populations of sand dollars, Dendraster excentricus (Eschscholtz). J. Exp. Mar. Biol. Ecol. 6: 265-278.

Byers, S. C., E. L. Mills and P. L. Stewart. 1978. A comparison of methods for determining organic carbon in marine sediments, with suggestions for a standard method. Hydrobiologia 58: 43-47.

Cassie, R. M., and A. D. Michael. 1968. Fauna and sediments of an intertidal mud flat: a multivariate analysis. J. Exp. Mar. Biol. Ecol. 2: 1-23.

Chia, F. S. 1969. Some observations on the locomotion and feeding of the sand dollar, Dendraster excentricus (Eschscholtz). J. Exp. Mar. Biol. Ecol. 3: 162-170.

Connell, J. H. 1961a. The influence of interspecific competition and other factors on the distribution of the barnacle Chthamalus stellatus. Ecology 42: 710-723.

Connell, J. H. 1961b. The effects of competition, predation by Thais lapillus, and other facotrs on natural populations of the barnacle, Balanus balanoides. Ecol. Monogr. 31: 61-104.

Connell, J. H. 1970. A predator-prey system in the marine

intertidal region. 1. Balanus glandula and several predatory species of Thais. Ecol. Monogr. 40: 49-78.

Davis, N., and G. R. Van Blaricom. 1978. Spatial and temporal heterogeneity in a sand bottom epifaunal community of invertebrates in shallow water. Limnol. Oceanogr. 23: 417-427.

Dayton, P. K. 1971. Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41: 351-389.

Dixon, W. J., and M. B. Brown, eds. 1977. BMDP-77. Biomedical Computor programs. P-Series. University of California Press, Berkeley, California. 880 pp.

Eagle, R. A. 1973. Benthic studies in the southeast of Liverpool Bay. Estur. Coast. Mar. Sci. 1: 285-299.

Ebert, T. A., and D. M. Dexter. 1975. A natural history study of Encope grandis and Mellita grantii, two sand dollars in the northern Gulf of California, Mexico. Mar. Biol. 32: 397-407.

Eleftheriou, A., and M. D. Nicholson. 1975. The effects of exposure on beach fauna. Cahiers Biol. Mar. 16(Suppl.): 695-710.

Ellis, D. V. 1971. A review of marine infaunal community studies in the Strait of Georgia and adjacent inlets. Syesis 4: 3-9.

Fager, E. W. 1957. Determination and analysis of recurrent groups. Ecology 38: 586-595.

Fager, E. W. 1964. Marine sediments: effects of a tube-building polychaete. Science 143: 356-359.

Fager, E. W. 1968. A sand-bottom epifaunal community of invertebrates in shallow water. Limnol. Oceanogr. 13: 448-464.

Frankenberg, D., and A. S. Leiper. 1977. Seasonal breeding cycles in benthic communities of the Georgia continental shelf. pp. 383-397 in B. C. Coull, ed. Ecology of marine benthos. Belle W. Baruch Lib. Mar. Sci. 6.

Green, R. H. 1971. A multivariate statistical approach to the Hutchinsonian niche: bivalve molluscs of central Canada. Ecology 52: 543-556.

Green, R. H., and K. D. Hobson. 1970. Spatial and temporal structure in a temporal intertidal community with

special emphasis on Gemma gemma (Pelecypoda: mollusca). Ecology 51: 999-1011.

Highsmith, R. 1977. Larval substrate selection, metamorphosis and mortality in the sand dollar, Dendraster excentricus. (Abstr.) Am. Zool. 17: 935.

Hulings, N. C., and J. S. Gray. 1971. A manual for the study of meiofauna. Smithsonian Contr. Zool. 78. 84pp.

Hutcheson, L. H. 1970. A test for comparing diversities based on the Shannon formula. J. Theor. Biol. 29: 151-154.

Johnson, R. G. 1970. Variations in diversity within benthic marine communities. Amer. Natur. 104: 285-300.

Jones, N. S. 1950. Marine bottom communities. Biol. Rev. 25: 283-313.

Kellerhals, P., and J. W. Murray. 1969. Tidal flats at Boundary Bay, Fraser River delta, British Columbia. Bull. Can. Petrol. Geol. 17: 67-91.

Levin, S. A., and R. T. Paine. 1974. Disturbance, patch formation and community structure. Proc. Nat. Acad. Sci. 71: 2744-2747.

Levings, C. D., and J. B. Coustalin. 1975. Zonation of intertidal biomass and related benthic data from Sturgeon and Roberts Banks, Fraser River Estuary, British Columbia. Fish. and Mar. Serv. Tech. Rep. 468. 138 pp.

Levinton, J. S. 1977. Ecology of shallow water deposit-feeding communities in Quisset Harbor, Massachusetts. pp. 191-225 in B. C. Coull, ed. Ecology of marine benthos. Belle W. Baruch Lib. Mar. Sci. 6.

Lie, U. 1974. Distribution and structure of benthic assemblages in Puget Sound, Washington, U. S. A. Mar. Biol. 26: 203-223.

Lie, U., and J. C. Kelley. 1970. Benthic infauna communities off the coast of Washington and in Puget Sound: identification and distribution of the communities. J. Fish. Res. Bd. Canada 27: 621-651.

Lie, U., and D. S. Kisker. 1970. Species composition and structure of benthic infauna communities off the coast of Washington. J. Fish. Res. Bd. Canada 27: 2273-2285.

Mac Ginitie, G. E. 1935. Ecological aspects of a California marine estuary. Am. Midl. Natur. 16: 629-765.

Mac Ginitie, G. E., and N. Mac Ginitie. 1968. Natural history of marine animals, second edition. Mc Graw-Hill Book Co., New York. 523 pp.

Mc Call, P. L. 1977. Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. J. Mar. Res. 35: 221-266.

Mc Cauley, J. E., and A. G. Carey, Jr. 1967. Echinoidea of Oregon. J. Fish. Res. Bd. Canada 24: 1385-1401.

Mc Grorty, S., A. Jenyon and R. Le B. Williams. 1976. Are hovercraft a major cause of disturbance to intertidal invertebrates? Biol. Conserv. 9: 13-20.

Merrill, R. J., and E. S. Hobson. 1970. Field observations of Dendraster excentricus, a sand dollar of western North America. Am. Midl. Natur. 83: 595-624.

Mills, E. L. 1967. The biology of an ampeliscid amphipod crustacean sibling species pair. J. Fish. Res. Bd. Canada 24: 305-355.

Mills, E. L. 1969. The community concept in marine zoology, with comments on continua and instability in some marine communities. J. Fish. Res. Bd. Canada 26: 1415-1428.

Moore, D. M. 1978. Seasonal changes in distribution of intertidal macrofauna in the Lower Mersey Estuary, U. K. Estur. Coast. Mar. Sci. 7: 117-125.

Nichols, F. H. 1970. Benthic polychaete assemblages and their relationships to the sediment in Port Madison, Washington. Mar. Biol. 6: 48-57.

Orr, H., J. C. Marshall, T. L. Isenhour, and P. C. Jurs. 1973. Introduction to computer programming for biological scientists. Allyn and Bacon, Inc., Boston.

Orth, R. J. 1977. The importance of sediment stability in seagrass communities. pp. 281-300 in B. C. Coull, ed. Ecology of marine benthos. Belle W. Baruch Lib. Mar. Sci. 6.

Paine, R. T. 1971. A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. Ecology 52: 1096-1106.

Paine, R. T. 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia 15: 93-120.

Pamatmat, M. M. 1966. The ecology and metabolism of a

benthic community on an intertidal sand flat (False Bay, San Juan Island, Washington). Ph. D. thesis. Univeristy of Washington. 243 pp.

Pamatmat, M. M. 1968. Ecology and metabolism of a benthic community on an intertidal sand flat. Intern. Rev. Ges. Hydrobiol. 53: 211-298.

Petersen, C. G. 1918. The seabottom and its production of fishfood. A survey of the work done in connection with valuation of the Danish waters from 1883-1917. Rep. Danish Biol. Sta. 25: 1-82.

Peterson, C. H. 1975. Stability of species and of community for the benthos of two lagoons. Ecology 56: 958-965.

Peterson, C. H. 1977. Competitive organization of the soft bottom macrobenthic communities of southern California lagoons. Mar. Biol. 43: 343-359.

Popham, J. D., and D. V. Ellis. 1971. A comparison of traditional cluster and Zurich-Montpellier analysis of infaunal pelecypod associations from two adjacent sediment beds. Mar. Biol. 8: 260-266.

Rhoads, D. C. 1967. Biogenic reworking of intertidal and subtidal sediments in Barnstable Harbor and Buzzards Bay, Massachusetts. J. Geol. 75: 461-476.

Rhoads, D. C., and D. K. Young. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. J. Mar. Res. 28: 150-178.

Rhoads, D. C., and D. K. Young. 1971. Animal-sediment relations in Cape Cod Bay, Massachusetts. II. Reworking by Molpadia oolitica (Holothuroidea). Mar. Biol. 11: 255-261.

Shelford, V. E., A. O. Weese, L. A. Rice, D. I. Rasmussen, A. Mac Lean, N. Wismer and H. Swanson. 1935. Some marine benthic communities of the Pacific coast of North America. Ecol. Monogr. 5: 251-354.

Sanders, H. L. 1958. Benthic studies in Buzzards Bay. I. Animal-sediment relationships. Limnol. Oceanogr. 3: 245-258.

Sanders, H. L. 1968. Marine benthic diversity: a comparative study. Am. Natur. 102: 243-282.

Sanders, H. L., E. M. Goudsmit, E. L. Mills and G. E. Hampson. 1962. A study of the intertidal fauna of Barnstable Harbor, Massachusetts. Limnol. Oceanogr. 7: 63-79.

Snedecor, G. W., and W. G. Cochran. 1967. Statistical methods, sixth edition. Iowa State Univ. Press, Ames, Iowa. 593 pp.

Sprules, W. G. 1977. Crustacean zooplankton communities as indicators of limnological conditions: an approach using principal component analysis. J. Fish. Res. Bd. Canada 34: 962-975.

Stephenson, W., W. T. Williams and S. D. Cook. 1972. Computer analyses of Petersen's original data on bottom communities. Ecol. Monogr. 42: 387-415.

Stephenson, W., W. T. Williams and G. N. Lance. 1970. The macrobenthos of Moreton Bay. Ecol. Monogr. 40: 459-494.

Thorson, G. 1957. Bottom communities. in J. W. Hedgepeth, ed. Treatise on marine ecology and paleoecology, Vol. 1. Geol. Soc. Amer. Memoir 67: 461-534.

Timko, P. L. 1975. High density aggregation in Dendraster excentricus (Eschscholtz): analysis of strategies and benefits concerning growth, age structure, feeding, hydronamics and reproduction. Ph. D. dissertation, Univ. of Calif. at Los Angeles. 305 pp.

Virnstein, R. W. 1977. The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. Ecology 58: 1199-1217.

Wieser, W. 1959. The effect of grain size on the distribution of small invertebrates inhabiting the beaches of Puget Sound. Limnol. Oceanogr. 4:181-194.

Williams, W. T., J. M. Lambert, and G. N. Lance. 1966. Multivariate methods in plant ecology. V. Similarity analyses and information analyses. J. Ecol. 54: 427-446.

Wiltse, W. I. 1977. Effects of predation by Polinices duplicatus (Gastropoda: Naticidae) on a sand-flat community. (Abstr.) Biol. Bull. 153: 450-451.

Woodin, S. A. 1974. Polychaete abundance patterns in a marine soft sediment environment: the importance of biological interactions. Ecol. Monogr. 44: 171-187.

Woodin, S. A. 1976. Adult-larval interactions in dense infaunal assemblages: patterns of abundance. J. Mar. Res. 34: 25-41.

Woodin, S. A. 1978. Refuges, disturbance and community structure: a marine soft bottom example. Ecology 59: 274-284.

Woodin, S. A., and J. A. Yorke. 1975. Disturbance, fluctuating rates of resource, recruitment and increased diversity. pp. 38-41 in S. A. Levin, ed. Ecosystem analysis and prediction. Soc. Industr. Appl. Math. Philadelphia, Pa.

Young, D. K., M. A. Buzas and M. W. Young. 1976. Species densities of macrobenthos associated with seagrass: a field experimental study of predation. J. Mar. Res. 34: 577-592.

Young, D. K., and D. C. Rhoads. 1971. Animal-sediment relations in Cape Cod Bay, Massachusetts. I. A transect study. Mar. Biol. 11: 242-254.

APPENDICES

Appendix 1. Treatment means (number/0.01-m^2 sample) of important False Bay infauna observed in the August, 1975, Dendraster-transfer experiment. The mean squared errors were obtained from nested analyses of variance. (*P<0.05; **P<0.01)

Species	No Cage	Empty Cage	Cage + 3 Dendraster	Cage + 6 Dendraster	MSE	F(3,4)
Leptosynapta	74.7	52.8	51.0	35.8	139.6	10.99*
Transennella	20.7	19.7	13.0	10.0	58.3	2.75
Paraphoxus spp.	508.2	550.0	588.2	542.2	34393.1	0.19
Pontogeneia	15.7	97.2	92.7	77.0	380.5	22.34**
Cumella	221.8	495.7	449.0	324.8	23697.2	3.88
Nebalia	3.2	1.3	1.3	1.7	1.2	3.80
Leptochelia	5.0	6.5	3.7	2.5	19.9	0.90
Leptochelia	24.5	14.7	5.3	5.5	347.6	1.43
Nemertopsis	18.2	4.3	4.5	3.0	9.2	33.09**
Lumbrineris	2.3	1.0	3.2	2.3	0.9	5.51
Onuphis	13.8	8.0	5.0	5.5	26.4	3.73
Spionidae spp.	34.8	45.2	44.7	47.0	375.2	0.48
Eusyllis?	4.8	8.0	10.2	8.8	47.3	0.65
Axiothella	1.5	1.0	1.5	2.0	1.8	0.57

Appendix 2. Treatment means (number/0.01-m^2 sample) of important False Bay infaunal species obtained in the June, 1975, *Dendraster*-exclusion experiment. MSE=mean squares for cages in the nested analyses of variance. (*P<0.05; **P<0.01)

Species	No Cage	*Dendraster* Cage	Empty Cage	MSE	F(2,3)
Leptosynapta	80.5	38.8	59.7	65.9	39.52**
Transennella	2.8	1.7	3.0	9.6	0.33
Paraphoxus spp.	281.5	243.5	235.8	6288.6	0.57
Pontogeneia	29.2	100.7	66.2	605.0	12.68*
Anisogammarus	23.7	3.8	1.7	13.8	63.76**
Cumella	138.2	55.2	70.7	786.1	14.86*
Nebalia	1.5	2.3	0.7	0.1	75.00**
Leptochelia	1.0	1.8	0.5	0.8	3.50
Leptochelia	2.2	0.7	0.7	6.3	0.72
Nemertopsis	1.3	1.8	1.3	3.8	0.13
Lumbrineris	2.7	1.3	2.0	2.4	1.09
Eusyllis?	19.3	13.3	11.3	45.6	2.28
Onuphis	1.3	0.5	0.2	3.7	0.59
Spionidae spp.	0.7	0.5	0.8	0.6	0.30

Appendix 3. Treatment means (number/0.01-m^2 sample) of important False Bay infaunal species obtained in the August, 1975, *Dendraster*-exclusion experiment. The mean squared errors were obtained from one-way analyses of variance. (*P<0.05; **P<0.01)

Species	No Cage	*Dendraster* Cage	Empty Cage	MSE	F(2,9)
Leptosynapta	99.0	34.2	44.8	63.3	76.34**
Transennella	37.0	13.0	11.8	23.4	34.59**
Paraphoxus spp.	530.8	450.0	529.8	3464.8	2.48
Ponotgeneia	11.0	21.0	12.2	42.1	2.82
Anisogammarus	1.8	1.8	1.8	3.4	0.00
Cumella	170.5	89.2	43.8	807.6	20.42**
Nebalia	1.8	3.8	2.0	3.9	1.20
Leptochelia	1.8	0.8	0.5	2.3	0.77
Leptochelia	3.5	0.5	2.8	2.8	3.54
Nemertopsis	10.8	0.8	1.2	8.9	14.24**
Lumbrineris	1.8	5.0	4.5	3.8	3.27
Eusyllis	22.5	10.8	19.8	43.4	3.48
Onuphis	0.5	1.0	2.0	1.4	1.62
Spionidae spp.	2.8	0.5	0.8	2.3	2.67

Appendix 4. Treatment means (number/0.01-m^2 sample) of selected False Bay infaunal species obtained in the June, 1976, *Dendraster*-exclusion experiment. Means for *Leptosynapta* were calculated from ln-transformed data. (**P<0.01)

Species	No Cage	*Dendraster* Cage	Empty Cage	MSE	F(2,20)
Leptosynapta	20.0	29.5	49.0	3.3	5.94**
Spionidae spp.	6.9	5.8	7.1	60.4	0.07

Appendix 5. Treatment means (number/0.01m^2-sample) of selected False Bay infaunal species observed in the August, 1976, *Dendraster*-exclusion experiment. The mean squared errors are based on factorial analyses of variance. (**P<0.01)

Species	No Cage	*Dendraster* Cage	Empty Cage	MSE	F(2,9)
Leptosynapta	27.0	20.7	11.0	7.7	50.81**
Transennella	5.2	1.5	4.3	7.3	3.02
Nebalia	1.3	3.8	1.5	9.2	1.27
Leptochelia	2.3	2.2	2.3	*	*

* ANOVA not performed